NASUTUCERATOPS TITUSI, A NEW BASAL CENTROSAURINE DINOSAUR (ORNITHISCHIA: CERATOPSIDAE) FROM THE UPPER CRETACEOUS KAIPAROWITS FORMATION, SOUTHERN UTAH

by

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STATEMENT OF THESIS APPROVAL

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ABSTRACT

Remains of a previously unknown horned dinosaur were recently recovered from the Upper Cretaceous (Campanian) Kaiparowits Formation of Grand Staircase-Escalante National Monument, southern Utah. These exceptionally preserved materials, including a nearly complete skull with multiple postcranial elements, represent a new genus and species of centrosaurine ceratopsid dinosaur, *Nasutuceratops titusi* n. gen. et n. sp. The new Utah taxon is placed within Centrosaurinae on the basis of multiple synapomorphies, including delta-shaped rostral; subcircular, hypertrophied narial region; thin, pronounced premaxillary septum; narial spine composed of processes from nasal and premaxilla; expanded and thickened ventral angle on premaxilla; and subrectangular, stepped squamosal. Autapomorhies of this taxon include ectonaris comprises 75% of preorbital skull length; nasals pneumatic; premaxilla-maxilla contact hyper-robust; double faceted, medially directed flange on maxilla contributing to short hard palette; and supraorbital horncores rostrolaterally directed, rostrally curved, torsionally twisted, and relatively enormous. A phylogenetic analysis of Centrosaurinae places *Nasutuceratops* as the sister taxon to *Avaceratops lammersi* from the late Campanian of Montana. *Nasutuceratops titusi* provides insights into the base of Centrosaurinae and suggests the existence of a previously unknown clade of short-snouted, long-horned centrosaurines in the southern Western Interior Basin (WIB) of North America. *Nasutuceratops* also provides strong support for hypothesis of dinosaur provinciality in late Campanian WIB.

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INTRODUCTION

Taxonomic Background

The monophyletic Ceratopsia represents one of the best known dinosaurian clades, with numerous genera described from complete or nearly complete skulls and skeletons (Marsh, 1891; Colbert, 1948; Currie and Dodson, 1984; Dodson, 1996; Sampson et al., 1997; Ryan and Russell, 2001; You and Dodson, 2004; Dodson et al., 2004; Sampson and Loewen, in press). Ceratopsids possess some of the most highly derived skulls among vertebrates (Fig. 1). Signature characteristics include the following: parrot-like beaks; dental batteries with shearing dentitions; hypertrophied narial regions; and ornamented parietosquamosal frills (Dodson et al., 2004; Sampson and Loewen, in press). Ceratopsia is composed of the basal Psittacosauridae, restricted to small-bodied Asian forms, and the larger-bodied Neoceratopsia, including the relatively enormous Ceratopsidae and a variety of more basal, midsized forms (Ryan et al., 2001; You and Dodson, 2004; Dodson et al., 2004; Fig. 2). Ceratopsidae is comprised of a diverse group of Late Cretaceous megaherbivores known from a relatively brief temporal distribution (~ 79 to 65 Ma; Sampson and Loewen, in press). They are typically subdivided into two monophyletic subclades ("subfamilies"): Chasmosaurinae, typically with simply adorned, elongate parietosquamosal frills (Lambe, 1915); and Centrosaurinae, typically with relatively shorter, highly adorned frills (Lambe, 1915; Dodson, 1993; Ryan et al., 2001, Sampson and Loewen, in press; Fig. 3). Additional

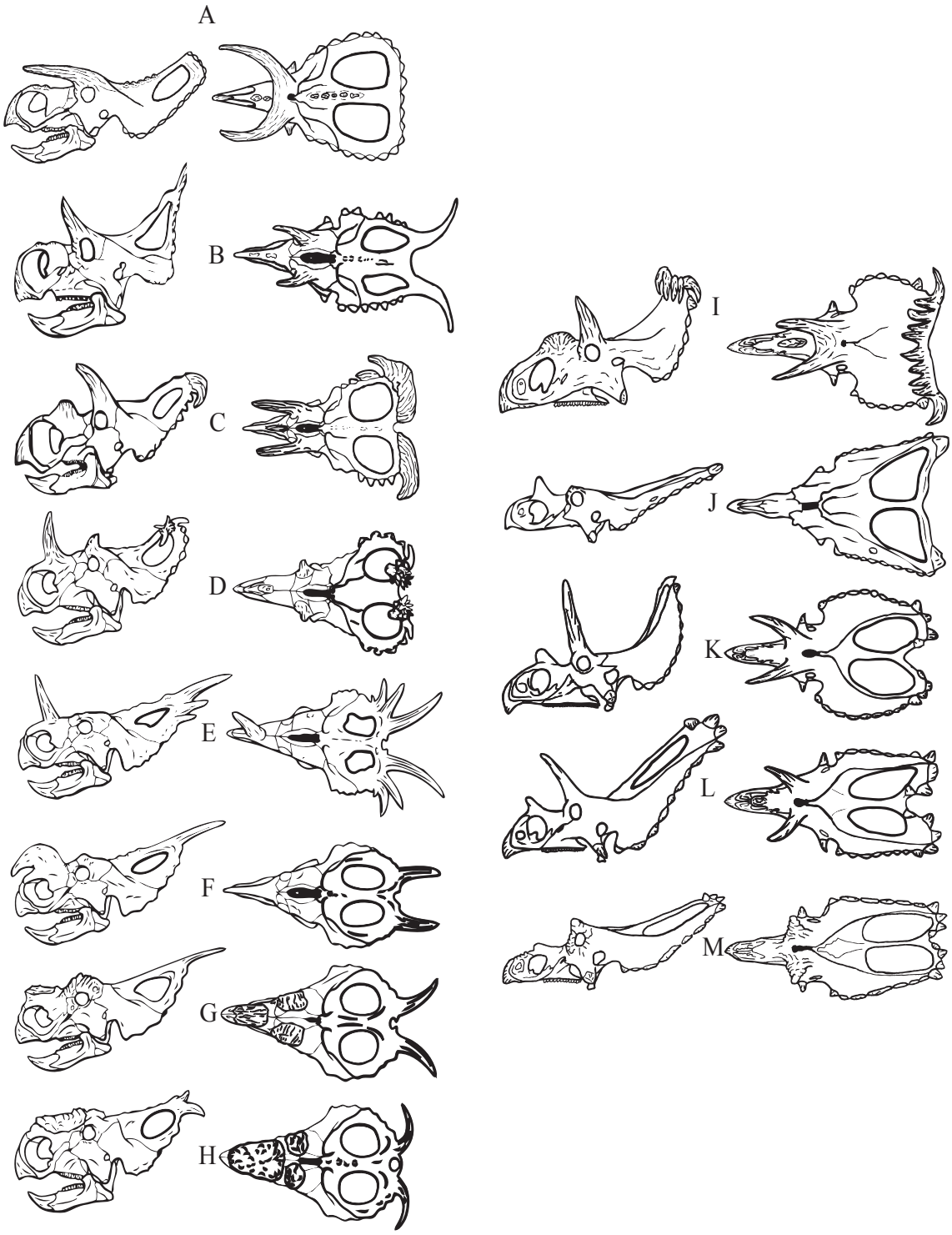

Figure 1. Diversity of ceratopsid skulls in Centrosaurinae (A-H) and Chasmosaurinae (I-M). Taxa indicated: **A**, *Nasutuceratops titusi*; **B**, *Diabloceratops eatoni*; **C**, *Albertaceratops nesmoi*; **D**, *Centrosaurus brinkmani*; **E**, *Styracosaurus albertensis*; **F**, *Einiosaurus procurvicornis*; **G**, *Achelousaurus horneri*; **H**, *Pachyrhinosaurus canadensis*; **I**, New Kaiparowits taxon A; **J**, *Chasmosaurtus belli*; **K**, *Agujaceratops mariscalensis*; **L**, *Pentaceratops sertnbergi*; **M**, New Kaiparowits taxon B

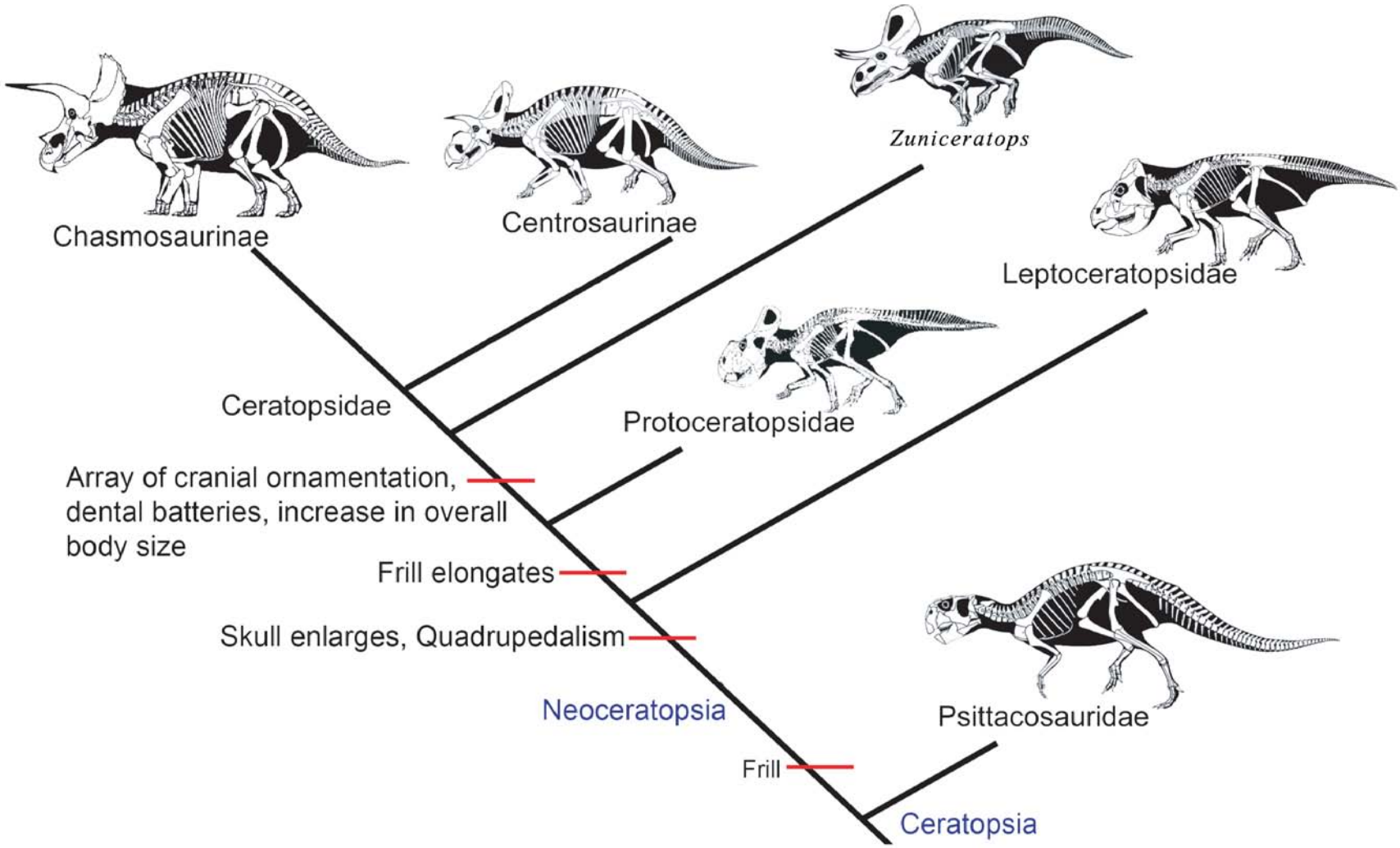

Figure 2. Cladistic relationships of Ceratopsia (after Holtz, 2006).

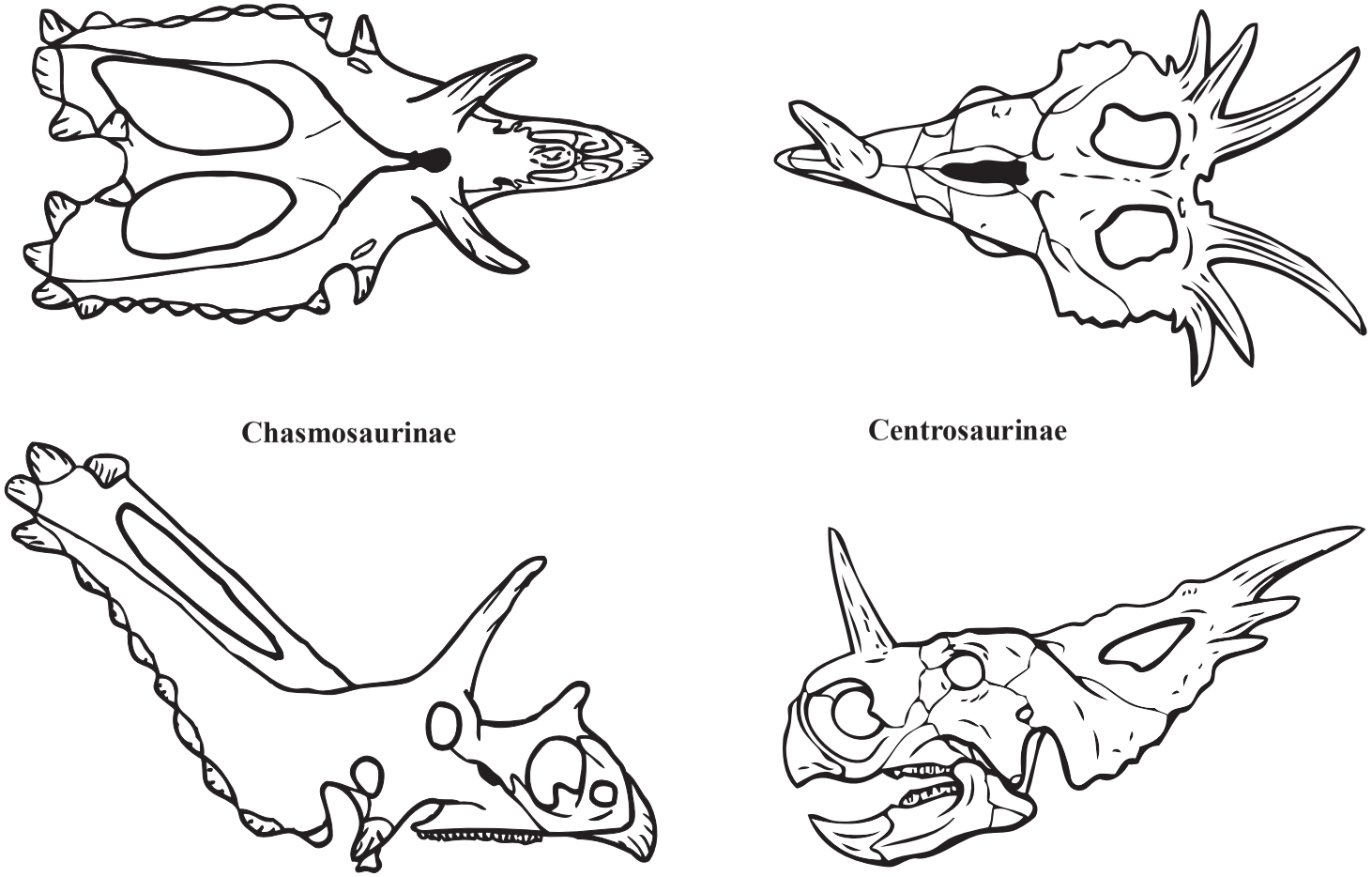

Figure 3. Subfamilies of Ceratopsidae--Centrosaurinae and Chasmosaurinae. Centrosaurines typified by long nasal ornamentation with short highly adorned parietosquamosal frills and marginal supraorbital ornamentation or pachyostotic bosses. Chasmosaurines typified by short nasal ornamentation with long parietosquamosal frills and supraorbital ornamentation (after Lehman, 1990).

characteristics typical of centrosaurines include well developed nasal horncores or bosses coupled with diminutive supraorbital horncores or bosses (Sampson et al., 1997; Sampson and Loewen, in press). Until recently, Centrosaurinae was generally split into two subclades, one containing *Centrosaurus* and *Styracosaurus* and the other containing *Einiosaurus*, *Achelousaurus*, and *Pachyrhinosaurus* (Sampson, 1995; Ryan, 2007). Description of two basal centrosaurines, however, indicates that elongate supraorbital horncores were a basal character of the group (Ryan, 2007; Kirkland and DeBlieux, in press). Previously recognized species within Centrosaurinae include *Achelousaurus horneri* Sampson, 1995, *Albertaceratops nesmoi* Ryan, 2007, *Avaceratops lammersi* Dodson, 1986, *Centrosaurus apertus* Lambe, 1904, *Centrosaurus brinkmani* Ryan and Russell, 2005 *Diabloceratops eatoni* Kirkland and DeBlieux, in press, *Einiosaurus procurvicornis* Sampson, 1995, *Pachyrhinosaurus canadensis* Sternberg, 1950, *Rubeosaurus ovatus* McDonald and Horner, in press, *Styracosaurus albertensis* Lambe, 1913, *Styracosaurus ovatus*, Gilmore, 1930 (Ryan, 2007; Sampson and Loewen, in press). Sampson et al. (1997), in their reexamination of *Brachyceratops montanensis* Gilmore, 1917 and *Monoclonius crassus* Cope, 1876, designated each a *nomen dubium* on the basis of ontogenetic evidence across multiple centrosaurine taxa. However, Tumarkin and Dodson (1998) reaffirmed the validity of *Monoclonius crassus* on the basis of heterochrony, suggesting that the putative subadult characters of the holotype are actually adult paedomorphic features. Ceratopsid taxonomy is based almost exclusively on characters of the skull roof, relating particularly to horns and frills, which are postulated to have rapidly evolved during the Late Cretaceous at least partially under the influence of sexual selection (Horner et al., 1992; Sampson, 1995; Sampson et al., 1997;

Dodson et al., 2004).

Excluding a *Pachyrhinosaurus*-like centrosaurine from the north slope of Alaska (Currie, 1989; Fiorillo and Gangloff, 2003) and a putative taxon from the Late Cretaceous of Uzbekistan (*Turanoceratops tardabilis*; Nessov et al., 1989), all of the aforementioned taxa—indeed all ceratopsids—have been found exclusively in sediments deposited in the Western Interior Basin (WIB) of North America (Parrish et al., 1987; Ryan, 2003; Blakey, 2009; Sampson and Loewen, in press; Fig. 4). The ceratopsid record in the southern region of the WIB (i.e., Utah, Colorado, New Mexico, Texas, and Mexico) has remained relatively poorly known and enigmatic compared to that of the north (i.e., Alberta, Saskatchewan, and Montana), resulting in a large latitudinal bias in the centrosaurine fossil record. Specifically, centrosaurines are known from numerous skulls and skeletons from the northern WIB, many of which occur in paucispecific bonebed assemblages (Ryan, 2007; Sampson and Loewen, in press). In contrast, only a limited number of isolated centrosaurine specimens are known from the southern WIB (Williamson, 1997; Heckert et al., 2003; Lund et al., 2007; Loewen et al., in press; Sullivan and Lucus, in press; Kirkland and DeBlieux, in press; Sampson and Loewen, in press).

New Dinosaurs from Grand Staircase-Escalante National Monument, Utah

Initiated by the University of Utah in 2000, the Kaiparowits Basin Project (KBP) is a multi-institution collaboration that has undertaken study of terrestrial and freshwater macrovertebrate fossils from two Campanian-aged geologic units within Grand Staircase-

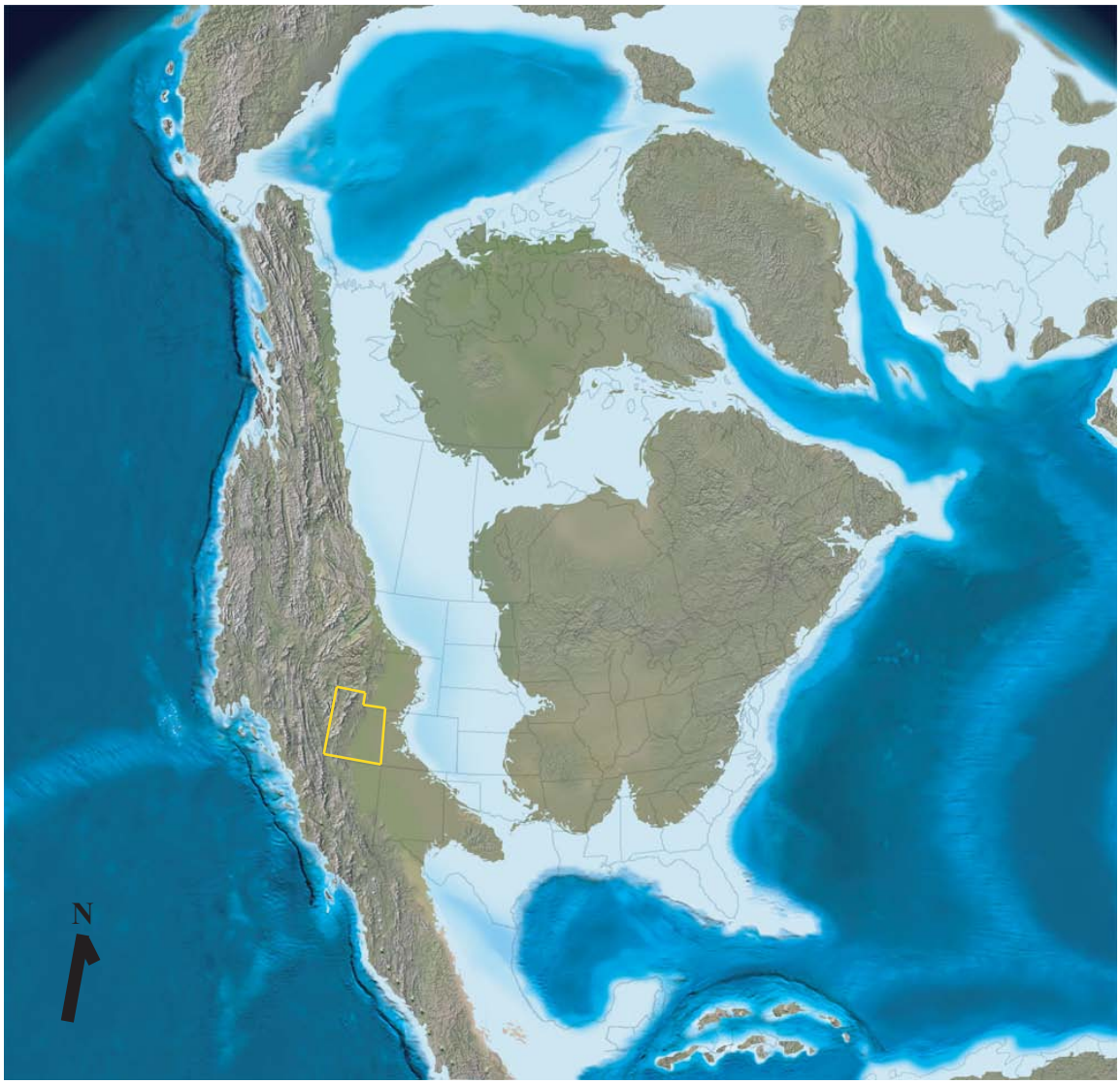

Figure 4. Map of the Western Interior Basin (WIB) 75 Mya. North America is at approximately 45º north paleolatitude. Yellow outline highlights approximate location of present day Utah (after Blakey, 2009).

Escalante National Monument (GSENM)—the Wahweap and Kaiparowits formations (Fig. 5). GSENM encompasses ~1.9 million acres of badland-type terrain formed from several Upper Cretaceous formations (Roberts, 2007). These formations represent one of the most contiguous Cenomanian-Campanian terrestrial records anywhere in the world (Eaton and Cifelli, 1988). From its initiation, the project has emphasized collection of macrovertebrates, predominantly dinosaurs, placing them into a well constrained stratigraphic and paleoenvironmental context (Roberts, 2005, 2007; Getty et al., in press).

Results of the KBP to date have been abundant and significant, documenting 16 nonavian dinosaur taxa within the Kaiparowits Formation alone. Two of these taxa have been formally named, the oviraptorosaur *Hagryphus giganteus* (Zanno and Sampson, 2006), and the hadrosaurine *Gryposaurus monumentensis* (Gates and Sampson, 2007). To date, greater than 70 partial to nearly complete skulls and skeletons of dinosaurs have been recovered, including tyrannosaurid, ornithomimid, and maniraptoran theropods; hypsilophodont, lambeosaurine and hadrosaurine ornithopods; nodosaurine and ankylosaurine ankylosaurids; and pachycephalosaurids (Sampson et al., in press). Prior to the inception of the KBP, ceratopsian remains from the Kaiparowits Formation were enigmatic, limited mostly to isolated teeth (Parrish and Eaton, 1991; Eaton et al., 1999; Roberts et al., 2003; Getty et al., in press). Since 2000, the KBP, combined with recent work conducted by the Utah Geologic Survey, has increased the known diversity of ceratopsids from the southern WIB by four genera and species, including two each of chasmosaurines and centrosaurines (Kirkland et al., 2002; Sampson et al., 2004; Kirkland and DeBlieux, in press; Sampson and Loewen, in press).

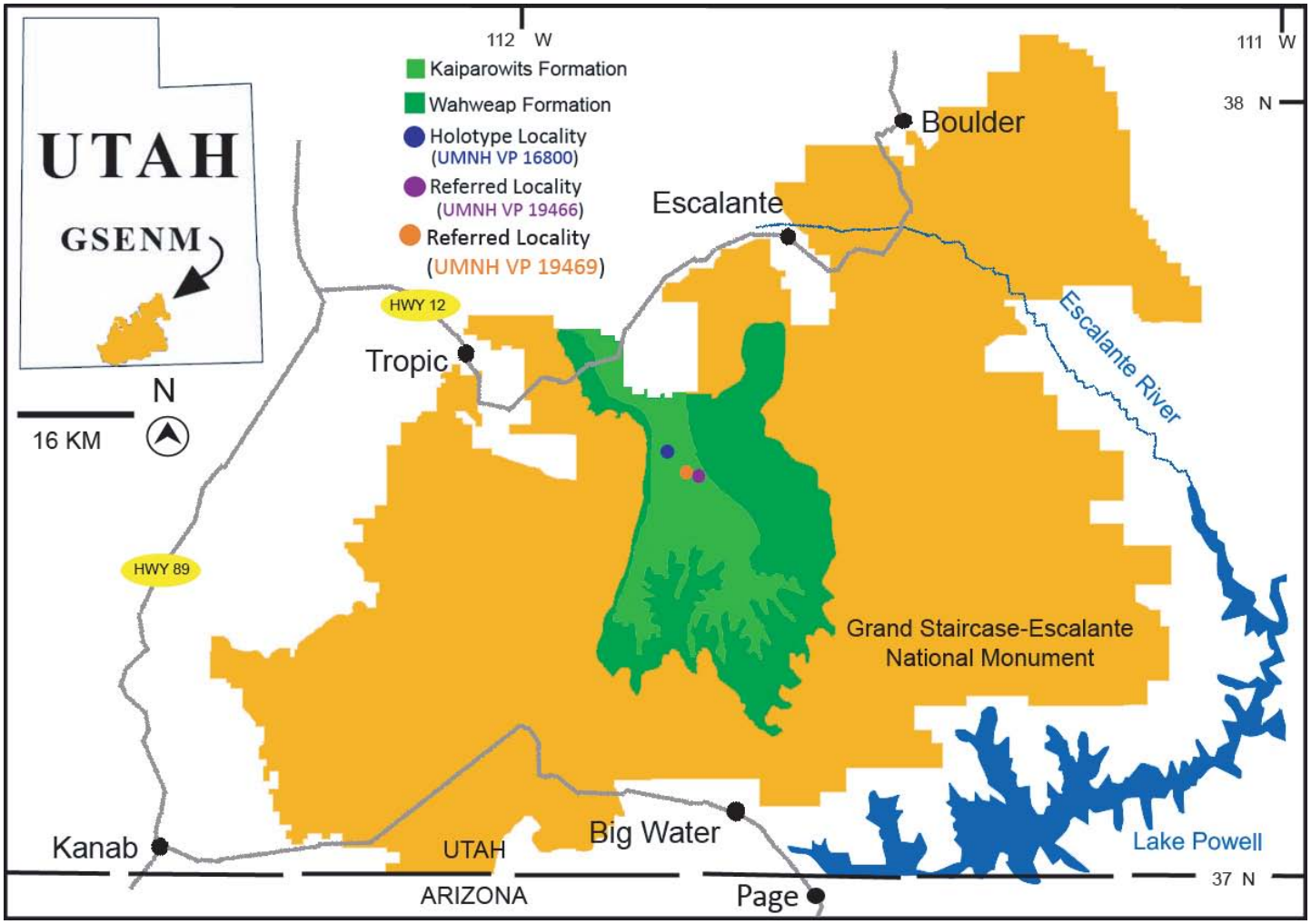

Figure 5. Generalized locality map of Grand Staircase-Escalante National Monument highlighting the Kaiparowits and Wahweap Formations (after Roberts et al., 2005).

Geologic Setting

Unless otherwise noted, the geologic summary below is derived from the work of Eric Roberts (Roberts et al. 2005; Roberts, 2007). The Kaiparowits Formation, which spans 76.1-74.0 Mya is an 860-m-thick clastic unit deposited as a mosaic of light gray floodplain and fluvial sediments. Expressed as badland-style exposures, the Kaiparowits Formation crops out over much of the northern portion of the Kaiparowits Basin, and represents approximately half of the 2-km-thick succession of Upper Cretaceous strata exposed on the Kaiparowits Plateau in GSENM (Fig. 5). Superficially, the formation appears to be mud-facies dominated, due in part to its slope-forming expression; however, the sandstone-to-mudstone ratio is typically closer to ~60:40.

The Kaiparowits Formation is part of a prograding clastic wedge that deposited vast quantities of sediment into the syn-evolving Sevier foreland basin (Goldstrand, 1992; Lawton et al., 2003; Roberts, 2007). The sandstone composition of the formation suggests that the sediment source for the basin was an advancing Late Cretaceous foreland fold-and-thrust belt approximately 300-500 km southwest of present day outcrops (Goldstand, 1992; Roberts, 2007). The sediments, which were deposited within a wet alluvial plain, consist of thick floodbasin pond and lake deposits, large fluvial channels, poorly developed hydromorphic paleosols, and paludal and riparian environments (Eaton, 1991; Roberts et al., 2005; Roberts, 2007).

The Kaiparowits Formation has been delineated into three informal stratigraphic units (lower, middle, upper) based on sedimentology and fossil preservation (Fig. 6). The lower unit (~0-170 m) is identified by a greater than 60% abundance of major sandstone facies, with less abundant minor sandstone facies interbedded with siltstone and

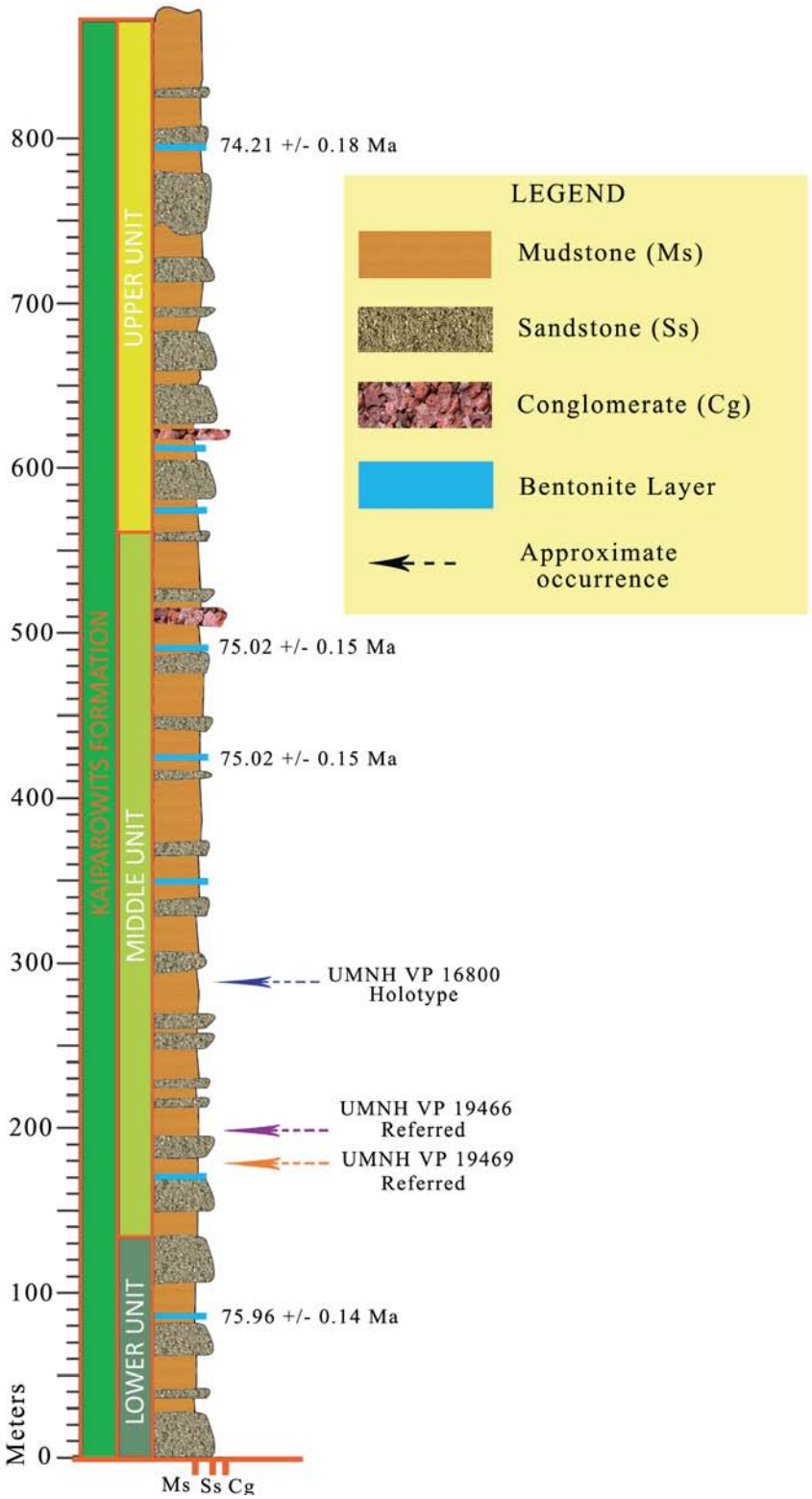

Figure 6. Composite measured section of the Kaiparowits Formation in Grand Staircase-Escalante National Monument. Approximate locations of the holotype material and referred material are shown to the right. Numbers to the right represent 40Ar/39Ar dates yielded from dated bentonite layers (after Roberts et al., 2005).

mudstone lenses. The middle unit (~170-550 m) contains considerably more muddy rich layers than either the lower or upper units, and is identified by a greater than 60% abundance of siltstone and mudstone, with less abundant interbedded sandstones, mudstones, and noncoalified organic mudstones. Additionally, pebble conglomerates with interbedded sandstones comprise a nominal component. Similar in character to the lower unit, the upper unit (~550-860 m) is identified by steeper topographic relief and higher induration than either the lower or middle units. There are five common fossiliferous lithofacies (Table 1) recognized within the Kaiparowits Formation: (1) pebble conglomerate; (2) major sandstone; (3) minor sandstone with interbedded mudstone; (4) siltstone and mudstone; and (5) noncoalified organic mudstone (Figs. 7-11).

The pebble conglomerate facies are dominated by intraformational siltstone and mudstone pebbles, with minor biogenic clasts (e.g., bone pebbles and invertebrate shells), and pedogenic carbonate nodules (Fig. 7). The beds are predominately lenticular, varying in thickness from 0.1-3 m, and are typically less than 25 m in lateral extent. These pebble conglomerate units have been interpreted as thalwag deposits in fluvial channels.

The major sandstone facies is characterized by texturally and compositionally immature, poorly sorted, fine-to-medium grained sands (Fig. 8). Bone, pebble, and wood clasts, including large trees with intact root balls, occur isolated throughout the facies. The beds are commonly tabular to lenticular in expression, range in thickness from 1.5 to >20 m, and have a lateral extent of 50-100 m or greater. Common bedding structures within the major sandstone facies include lateral accretion, trough and tabular cross-beds, and planar and convoluted bedding. These major sandstone deposits have been

Table 1. Five common fossiliferous lithofacies identified within the Kaiparowits formation		
#	**Lithofacies Name**	**Description**
1	Pebble Conglomerate	Matrix to clast supported facies, light brown to gray, dominated by intra-formational siltstone and mudstone pebbles, with minor biogenic clasts (e.g., bone pebbles and invertebrate shells), and pedogenic carbonate nodules. Bedformes are typically lenticular, varying in thickness from 0.1-3 m and are typically less than 25 m in lateral extent
2	Major Sandstone	Immature, poorly sorted, fine-to-medium grained sands. Bone, pebble, and wood clasts, including large trees with intact root balls, occur isolated thoughout the facies. Bedformes are tabular to lenticular and range in thickness from 1.5 to >20 m and have a lateral extent of 50-100 m or greater
3	Minor Sandstone	Immature, poorly sorted, fine-to-medium grained sands. Bedformes are tabular to lenticular and range in thickness from 2-20 m and have a lateral extent of tens of meters to kilometers. This facies exhibites evidence of moderate to intense bioturbation and rhizoturbation.
4	Siltstone and Mudstone	Composed of amalgamated siltstone, silty-mudstone, sandy-mudstone, and muddy sandstone beds ranging in thickness from 0.3-0.7 m with a lateral extent of tens of meters to hundreds of meters. Facies is characterized by a gray-green color indicative of hydromorphic soil formation.
5	Noncoalified organic mudstone	Finely laminated dark brown, carbonaceous claystones ranging in thickness from 0.3-0.75 m with a lateral extent of 10-300 m

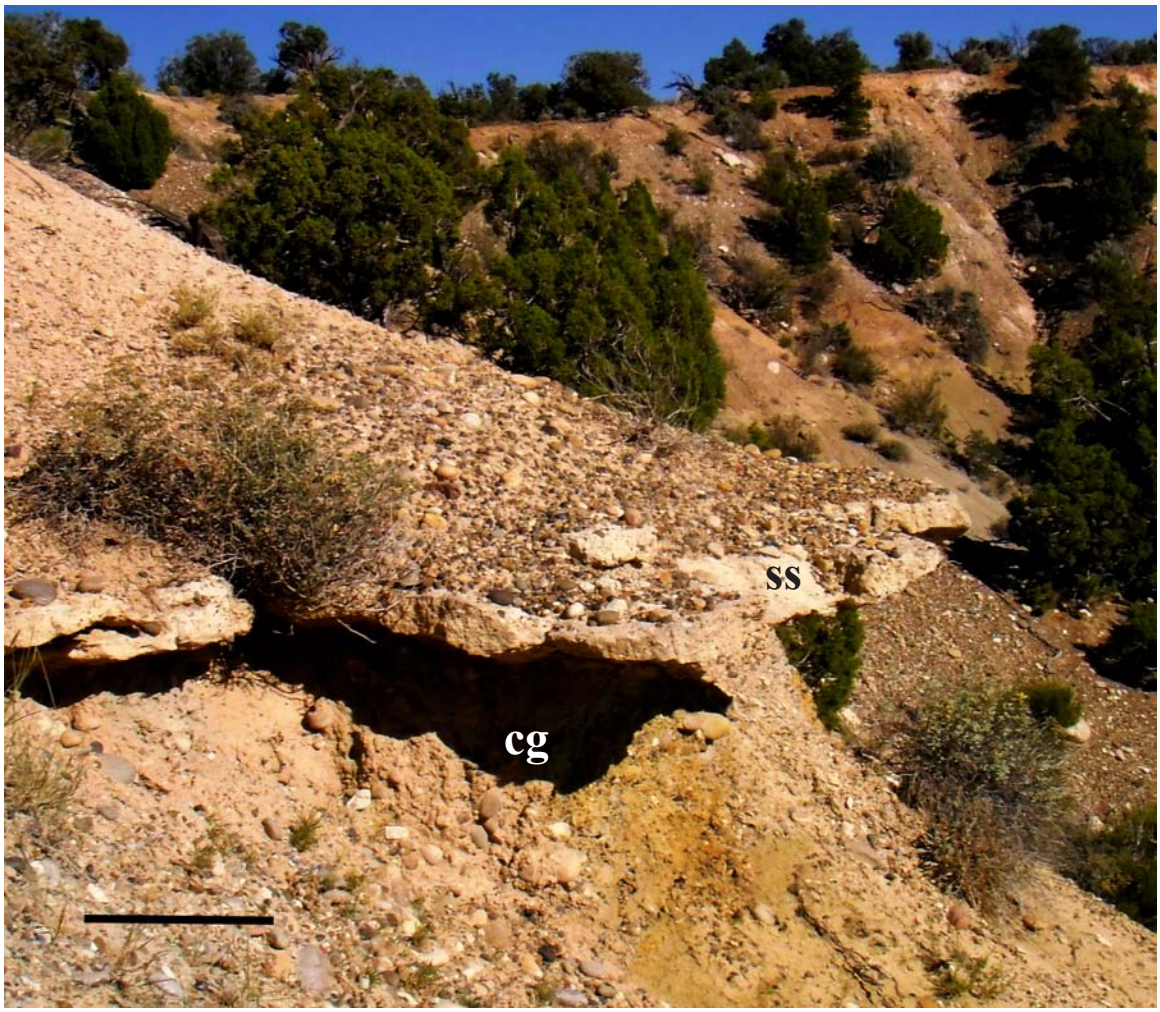

Figure 7. Photograph of the pebble conglomerate lithofacies in the Kaiparowits Formation, which is one of five common fossiliferous lithofacies recognized in the formation. **Abbreviations**: **cg**, conglomerate; **ss**, sandstone. Scale bar = 1m.

Figure 8. Photograph of the major sandstone lithofacies in the Kaiparowits Formation, which is one of five common fossiliferous lithofacies recognized in the formation. **Abbreviations**: **ms**, mudstone; **ss**, sandstone. Scale bar = 1m.

interpreted as meandering and anastamosing fluvial channel deposit.

The minor sandstone with interbedded mudstone facies is compositionally and texturally similar to the major sandstone facies, being texturally and compositionally immature, poorly sorted, composed of fined to medium-grained clasts (Fig. 9). The beds typically range from 2-20 m in thickness, and have a typical lateral extent of tens of meters to kilometers. Common bed forms include planar and ripple laminations. There is also evidence of moderate to intense bioturbation, and rhizoturbation. This facies has been interpreted to represent a myriad of fluvial environments, including levee, crevasse splay, channel, and channel fill. However, poor induration of this facies has made precise paleoenvironmental interpretations difficult to ascertain.

The siltstone and mudstone facies are typically composed of amalgamated siltstone, silty-mudstone, sandy-mudstone, and muddy-sandstone beds ranging in thickness from 0.3-0.7 m, with a typical lateral extent ranging from tens of meters to hundreds of meters (Fig. 10). The siltstone and mudstone facies have been interpreted as floodbasin deposits, which manifest as ephemeral pond and lake deposits, paleosols, channel fill, and altered ash layers. The paleosols are characterized by poor development, minor incipient caliche formation, slickensides, gleying, and weak color banding. In addition to the aforementioned characters, the facies-consistent gray-green hue is indicative of hydromorphic soils (gleysols), suggestive of formation in a relatively wet, sub-tropical environment.

The noncoalified organic mudstone facies are sparse relative to the other major fossiliferous facies (Fig. 11). However, they are extremely important for elucidating the paleoenvironmental and depositional history of the Kaiparowits Formation. The facies is

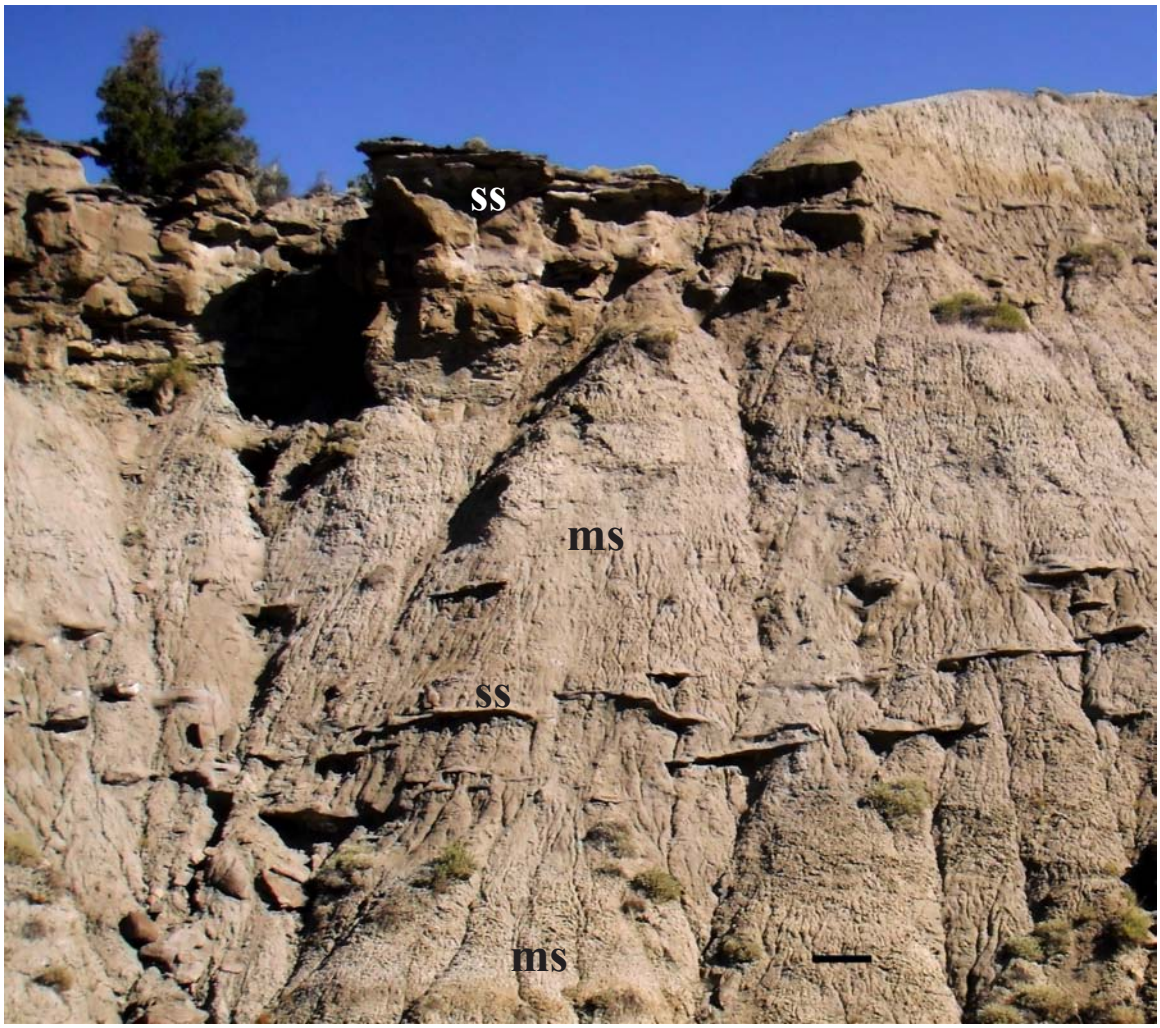

Figure 9. Photograph of the minor sandstone with interbedded mudstone lithofacies in the Kaiparowits Formation, which is one of five common fossiliferous lithofacies recognized in the formation. **Abbreviations**: **ms**, mudstone; **ss**, sandstone. Scale bar = 1m.

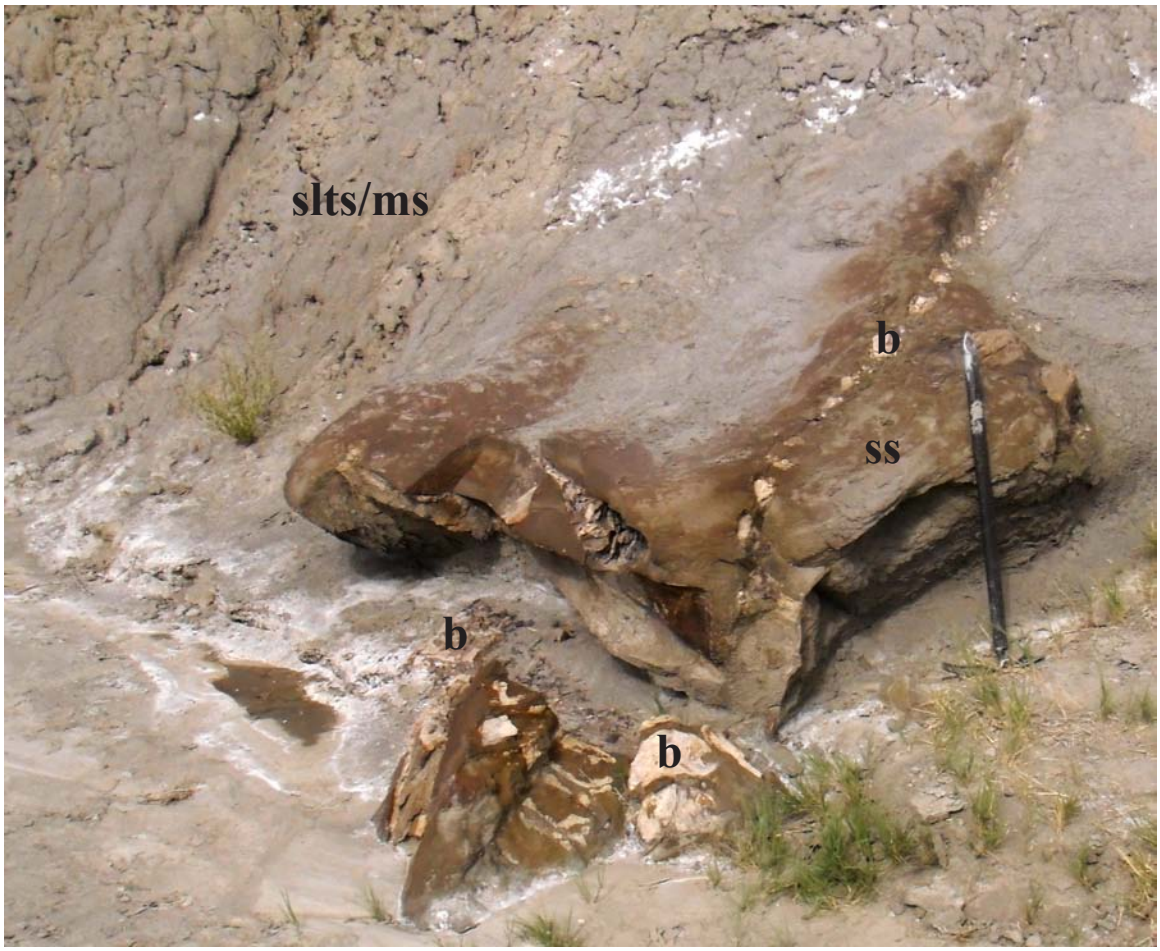

Figure 10 Photograph of the siltstone and mudstone lithofacies in the Kaiparowits Formation, which is one of five common fossiliferous lithofacies recognized in the formation. **Abbreviations**: **b**, bone; **ms**, mudstone; **slts**, siltstone; ss, sandstone. Cream colored patches in photograph are the fossil remains of a large hadrosaurid. Ice axe on bottom right for scale is 70 centimeters long.

Figure 11. Photograph of the noncoalified organic mudstone lithofacies in the Kaiparowits Formation, which is one of five common fossiliferous lithofacies recognized in the formation. **Abbreviations**: **ms**, mudstone; **slts**, siltstone; **ss**, sandstone. Scale bar = 3m.

characterized by finely laminated (rarely massive) dark brown, carbonaceous claystone beds, which range in thickness from 0.3-0.75 m, and are typically 10-300 m in lateral extent. The amount of recognizable macroscopic biogenic material (fossils) contained within this facies is highly variable between individual beds. Several beds are totally devoid of biogenic materials, whereas others contain abundant fragments of carbonized plant, freshwater shells, and vertebrate fossils.

New Ceratopsid Dinosaur from Grand Staircase-Escalante National Monument, Utah

This report focuses on three specimens of a new centrosaurine horned dinosaur recovered from fluvial sandstone facies within the informal middle unit of the Kaiparowits Formation. The holotype of this new taxon (UMNH 16800) was recovered from the top of a small knoll entombed in fine-grained fluvatile sandstone. The surrounding matrix is moderately mature, being well sorted and subrounded, suggestive of a moderate energy fluvial environment such as a sandbar or point bar deposit. Additionally, lenses of coarse grained rip-up clast conglomerate are randomly dispersed throughout the sandstone, hinting at uncommon increases in fluvial energy, such as occasional storm surges. This observation is substantiated by fragmented, coalified botanical remains incorporated throughout the matrix. Taphonomically, the specimen was positioned with the cranial portion trending into the hill and the postcranial skeleton trending out of the hill. Unfortunately, the bulk of the postcranial skeleton was not preserved. Additionally, many of the craniofacial elemenets were broken predepositionally and displaced from life position (Fig. 12).

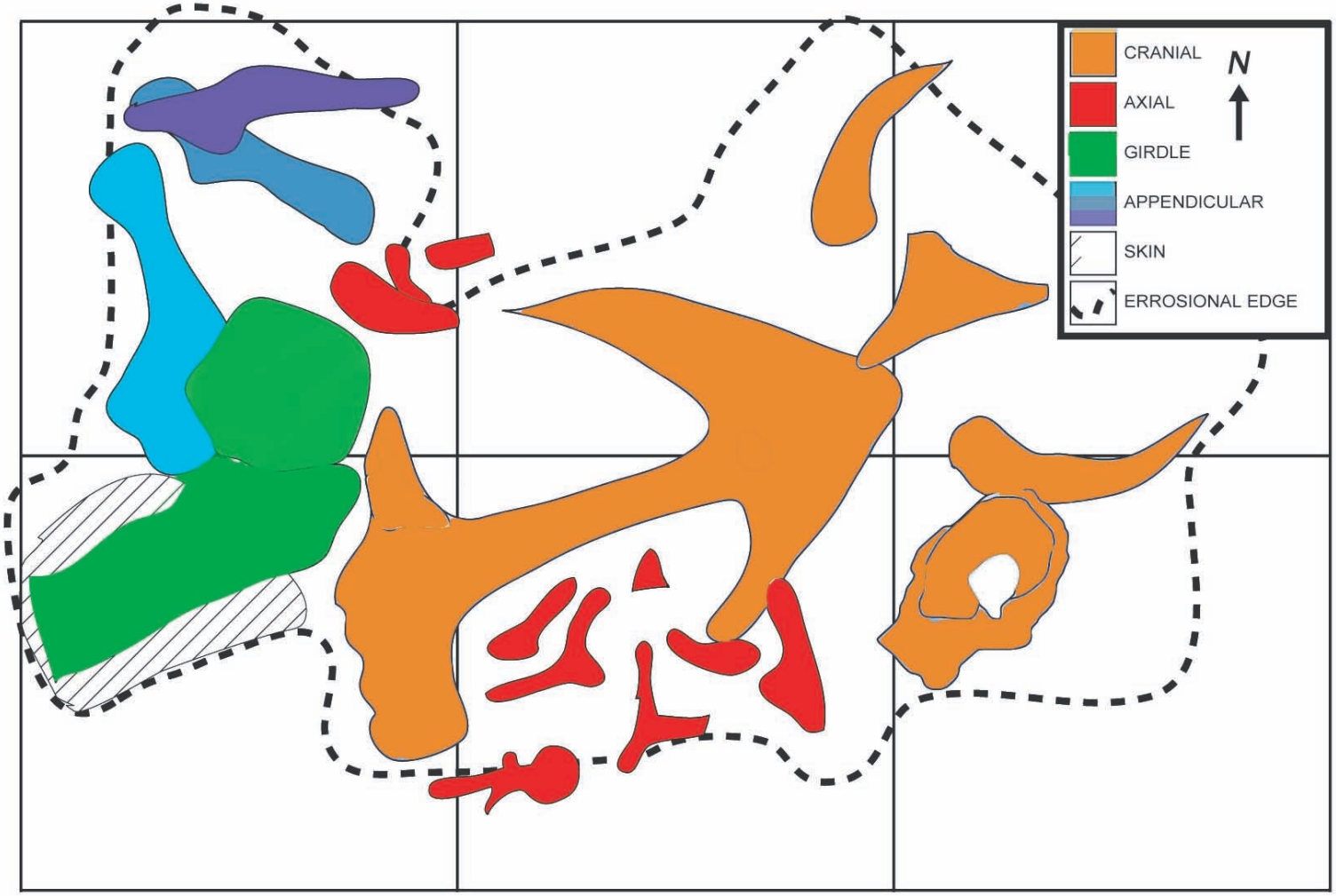

Figure 12. Generalized holotype quarry map for *Nasutuceratops titusi* gen. et sp. nov., colors used correspond to colors in Figure 14. Each square in grid equals 1 square meter.

The referred material comes from a multitaxic bonebed, preserving portions of an ankylosaur and elements of the new centrosaurine. The entombing matrix consists of indurated, fluviatile sandstone interbedded with coarse-grained lenses of rip-up clast conglomerate, suggestive of a large channel lag deposit. The matrix contains abundant fragmented, charcoalified botanical material along with isolated and fragmented turtle, fish, and crocodile elements. Additionally, every preserved element from the new centrosaurine was predepositionally fragmented and diarticulated, suggestive of deposition in a channel lag.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, NY; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MOR**, Museum of the Rockies, Bozeman, MT; **MSM**, Mesa Southwest Museum, Mesa, AZ; **NMC**, Canadian Museum of Nature (National Museum of Canada), Ottawa, Ontario; **NMMNH**, New Mexico Museum of Natural History, Albuquerque, NM; **ROM**, Royal Ontario Museum, Toronto, Ontario; **TMP**, Royal Tyrrell Museum of Paleontology; Drumheller, Alberta; **UMNH VP**, Utah Museum of Natural History Vertebrate Paleontology Collection, Salt Lake City, UT; **UTEP**, University of Texas, El Paso, TX; **YPM**, Yale Peabody Museum, New Haven, CT; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

MATERIALS AND METHODS

This study represents details of three previously undescribed specimens pertaining to a new horned dinosaur recovered from the Kaiparowits Formation. The holotype (UMNH VP 16800) consists of a nearly complete skull preserving much of the skull roof; a nearly complete syncervical; a complete left forelimb together with associated nonmineralized soft-tissues; and a fragmentary right forelimb including portions of the scapula, humerus, ulna and radius; and fragmentary dorsal vertebrae and ribs. A second specimen (UMNH VP 19466) consists of a disarticulated skull, including the ventral portions of the left and right premaxillae, and a nearly complete right maxilla and nasal. The third specimen (UMNH VP 19469) is a virtually complete isolated right squamosal. All specimens are curated in collections of the Utah Museum of Natural History, Salt Lake City, Utah.

The anatomical description and phylogenetic analysis methods employed during this study are standard protocols used for analysis of fossil vertebrates. The phylogenetic character codings and morphological descriptions were obtained primarily from firsthand specimen observations, but augmented with the primary literature where required.

SYSTEMATIC PALEONTOLOGY

Ceratopsia Marsh, 1890

Ceratopsidae Marsh, 1888

Centrosaurinae Lambe, 1915

Nasutuceratops titusi gen. et sp. nov.

Etymology.— "*Nasutus*" (Latin) describes the specimen as "large-nosed" + *ceratops* (Latinized Greek) describes the specimen as "horned-face". The specific name *titusi* is a patronym in honor of GSENM paleontologist, Alan Titus, who has played a pivotal role in the recovery of fossils from GSENM.

Diagnosis.—Centrosaurine possessing the following autapomorphies: external naris comprises 75% of the preorbital skull length; nasals pneumatic; premaxillary contact of the maxilla hypertrophied, forming an expanded contact shelf; maxilla with double faceted, medially directed flange contributing to hard palette; supraorbital horncores rostrolaterally directed, rostrally curved, and torsionally twisted. *Nasutuceratops* is also characterized by the following unique suite of synapomorphies: squamosal with pronounced dorsolateral ridge; subrectangular parietosquamosal frill with simple crescentic episquamosals and epiparietals; epiparietal positions p0-p7, with epiparietal position p0 being generally unique among centrosaurines, only occurring in one other centrosaurine (i.e., *Avaceratops lammersi*).

Holotype.—Utah Museum of Natural History (UMNH) VP 16800, a partially associated nearly complete skull about 1.5 m long, together with an associated left forelimb.

Referred material.—UMNH VP 19466, a disarticulated adult skull including a partial premaxilla, maxilla and nasal; UMNH VP 19469, an isolated squamosal.

Localities and horizon.—GSENM, southern Utah, USA. Stratigraphically, *Nasutuceratops* occurs within the middle unit (~250-320 m) of the upper Campanian Kaiparowits Formation, dated between ~75.9-75.2 Ma (Roberts et al., 2005; Roberts, 2007). Detailed locality information on file at the UMNH.

DESCRIPTION

The holotype skull of *Nasutuceratops titusi* gen. et sp. nov. (UMNH VP 16800) is largely complete, preserving most of the skull roof (Fig. 13). The specimen is interpreted as a subadult individual based on fusion of skull elements and bone surface texture (Sampson et al., 1997). Two additional specimens are here referred to this taxon. Considered together, these materials represent approximately 80% of the craniofacial skeleton and approximately 10% of the postcranial skeleton (Fig. 14). Genus and species level taxonomic resolution of ceratopsids has typically been defined on craniofacial characters pertaining to the skull roof (Dodson et al., 2004). Therefore, this description is limited to skull characters derived primarily from the holotype specimen. The description is subdivided into three main sections—circumnarial region; circumorbital region; and parietosquamosal frill—with each section focusing on key aspects useful in resolving taxonomic relationships of centrosaurines.

Craniofacial Skeleton

The nasal and premaxilla dominate the circumnarial region, but for ease of description, both the rostral and maxilla are included in this section. *Nasutuceratops* possesses a remarkably tall (deep) craniofacial skeleton, particularly in the circumnarial region (Fig. 15). The deep facial skeleton is similar to that described for *Diabloceratops* (UMNH VP 16699; Kirkland and DeBlieux, in press). Overall, the narial region of

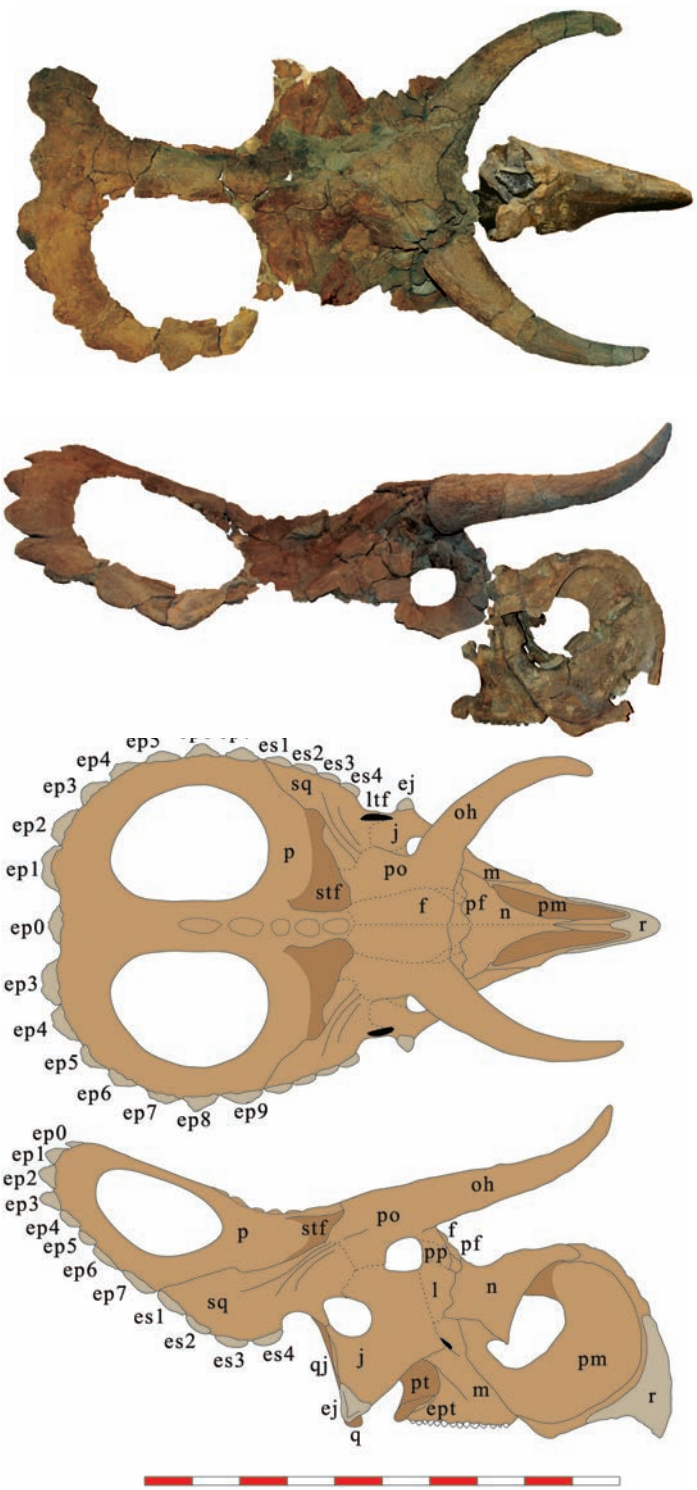

Figure 13. Dorsal and lateral views of *Nasutuceratops titusi* gen. et sp. nov. with reconstruction. **Abbreviations**: **ej**, epijugal; **ep**, epiparietal; **ept**, ectoterygoid; **es**, episquamosal; **f**, frontal; **j**, jugal; **l**, lacrimal; **ltf**, lateral temporal fenestra; **m**, maxilla; **n**, nasal, **oh**, orbital horn; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pp**, palpebral; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **r**, rostral; **sq**, squamosal; **stf**, supratemporal fenestra. Scale bar = 1 m.

Figure 14. Skeletal reconstruction of *Nasutuceratops titusi* gen. et sp. nov. Colored elements represent elements recovered.from holotype quarry. Colors correspond to Figure 12. (quarry map). Scale bar = 1m.

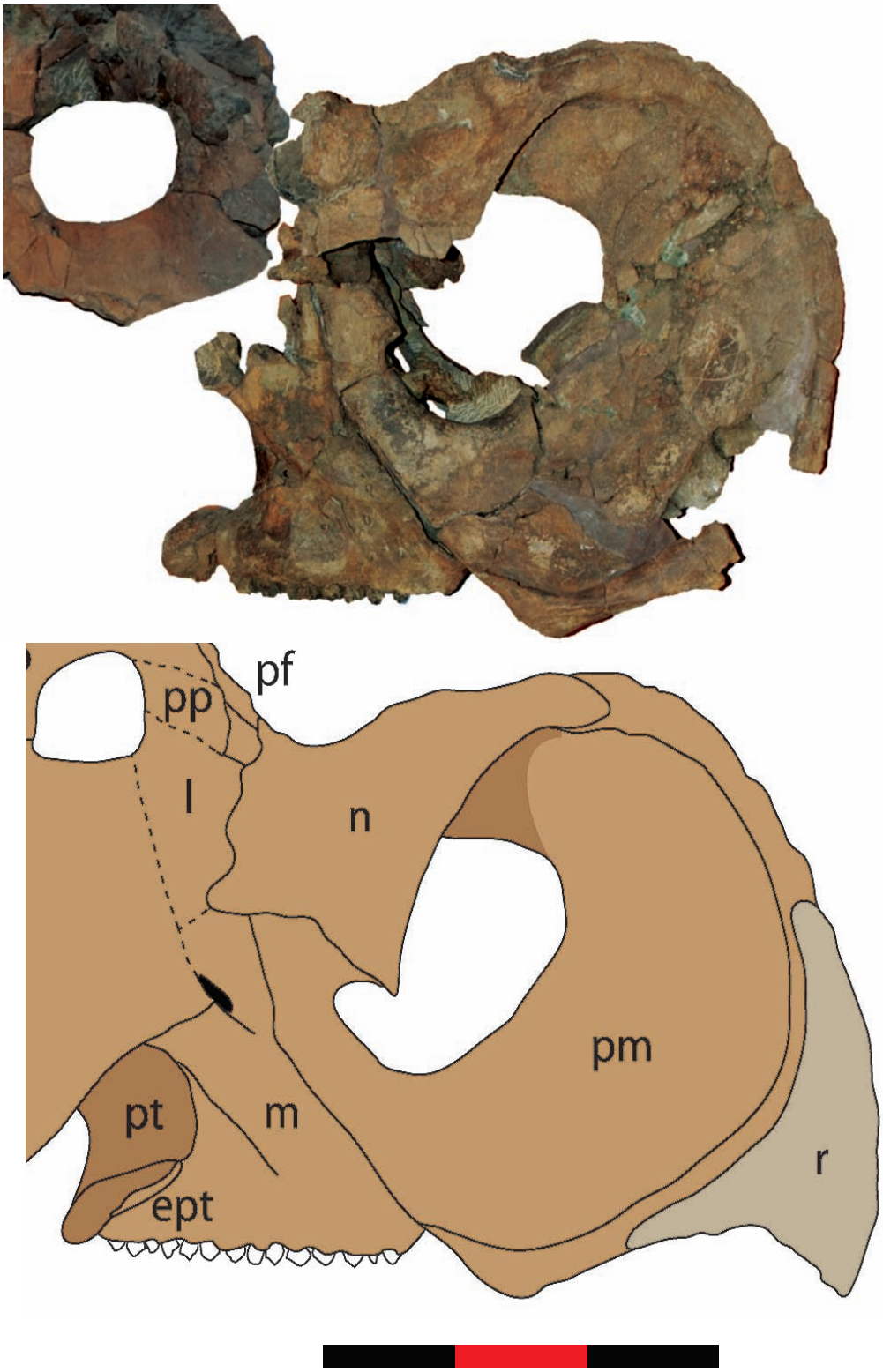

Figure 15. Photograph with reconstruction of the circumnarial region. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 16800. **Abbreviations**: **ept**, ectopterygoid; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pf**, prefrontal; **pp**, palpebral; **pt**, pterygoid; **r**, rostral. Scale bar = 30 cm.

Nasutuceratops is subcircular in shape, typical of centrosaurines (e.g., *Achelousaurus*, MOR 485; *Einiosaurus*, MOR 456). However, it differs from all more derived centrosaurines, and is similar to *Diabloceratops*, in being dorsally expanded such that the narial region possesses a bulbous appearance.

Circumnarial Region

Rostral

The rostral, a neomorphic element of Ceratopsia, contacts the rostralmost portion of the premaxilla in ceratopsids, forming the upper portion of the beak (Fig. 15). Although the rostral is not preserved with *Nasutuceratops* UMNH VP 16800, the general conformation of this element can be inferred from the preserved scar on the premaxilla (Fig. 16). The preserved contact surface is rugose, typical of other ceratopsids, and crescentic in shape, closely following the contours of the narial border. The upper extent of the dorsal ascending prong was approximately level with the middle of the narial opening whereas the caudal extent of the caudolateral ventral prongs nearly abutted against the ventral angle of the premaxilla. Based on this conformation, as well as the shape of this element in centrosaurines generally, the rostral in *Nasutuceratops* is here interpreted as being a delta-shaped, triangular element as viewed laterally, similar to the condition in *Diabloceratops* (UMNH VP 16699) and *Centrosaurus* (AMNH 5259), and differing from that present in *Zuniceratops* (MSM P2101) and Chasmosaurines.

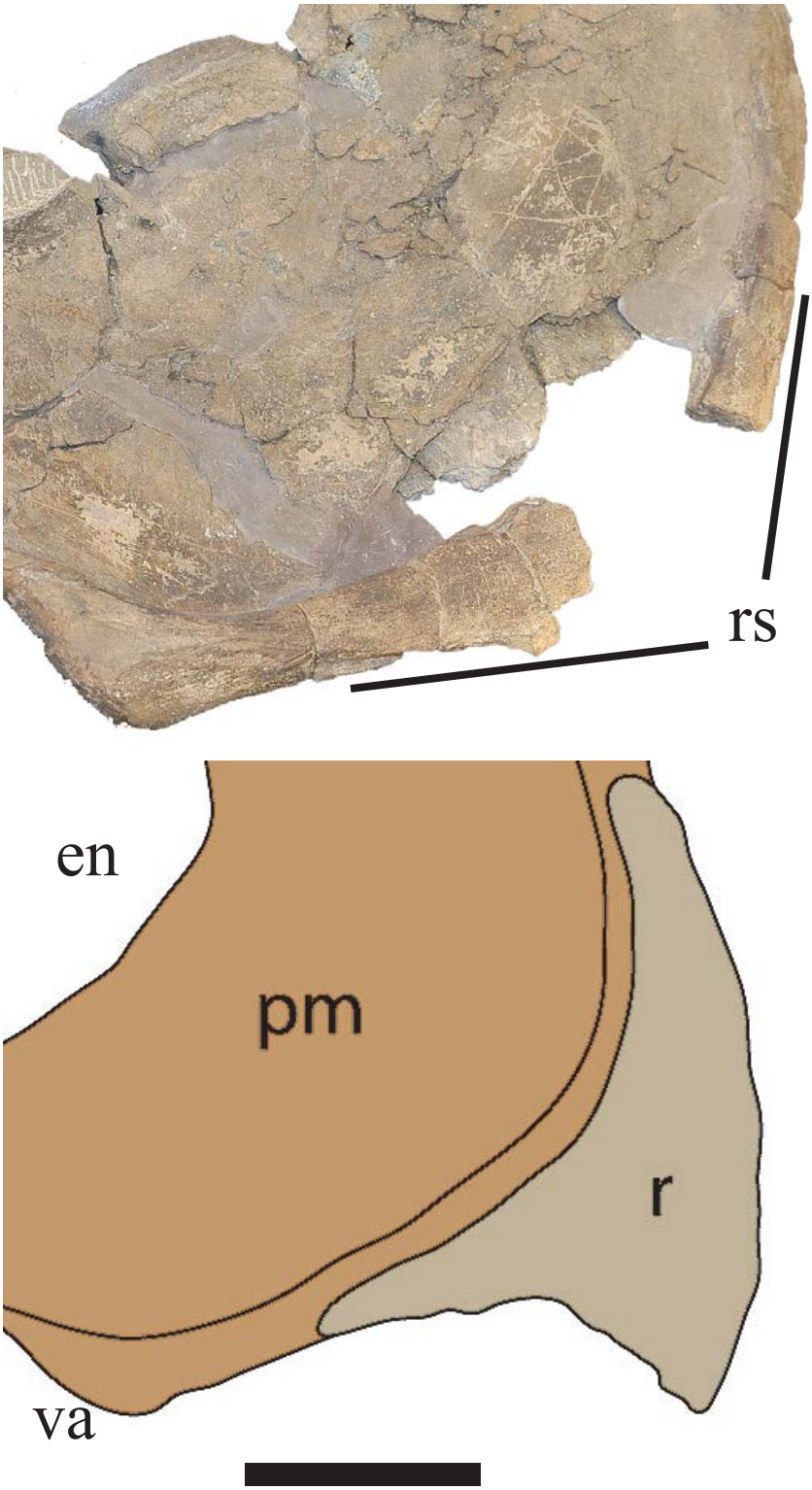

Figure 16. Photograph with reconstruction of the rostral scar on the premaxilla. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 16800. **Abbreviations**: **en**, endonaris; **pm**, premaxilla; **r**, rostral; **rs**, rostral scar; **va**, ventral angle. Scale bar = 10 cm.

Premaxillae

Portions of both premaxillae, preserved in contact with each other as well as with the nasals, are present in *Nasutuceratops* UMNH VP 16800, but are damaged and transversely crushed, with the right side missing much of its ventral half (Fig. 17). Additionally, partial right and left premaxillae (UMNH VP 19466.3, UMNH VP 19466.4) very similar to the holotype were recovered from another quarry and are here referred to *Nasutuceratops* (Figs. 18, 19). Whereas the premaxilla of centrosaurines tends to be morphologically conservative, this element in *Nasutuceratops* possesses several characteristics that distinguish it from other centrosaurines.

In general, the premaxilla of this new taxon closely resembles that of other centrosaurines (e.g., *Centrosaurus*, *Styracosaurus*) in being roughly subcircular, with a well developed premaxillary septum and a thick, downward projecting ventral angle. The ectonarial recess (deep invaginated channel running along the rostroventral margin of the premaxilla), well preserved on the left side of UMNH VP 16800, is deep and separates the premaxillary septum from the more robust lateral border. As in other ceratopsids, the premaxillae is edentulous and contacts the rostral rostrally, the maxilla caudoventrally, the nasal dorsally, and the lacrimal caudodorsally (Sampson, 1995). The premaxillae are thin and blade-like, typical of other centrosaurines; however, this element is exceptionally tall in *Nasutuceratops*, contributing to the exceptionally deep facial skeleton (Sampson, 1995; Kirkland and DeBlieux, in press). In lateral view, the rostrodorsal margin of the premaxilla, just rostral to the contact with the nasals, is medio laterally pinched and raised dorsally, creating a bulbous hump in front of the nasal horncore (Fig. 15). A similar conformation of the narial region is present in

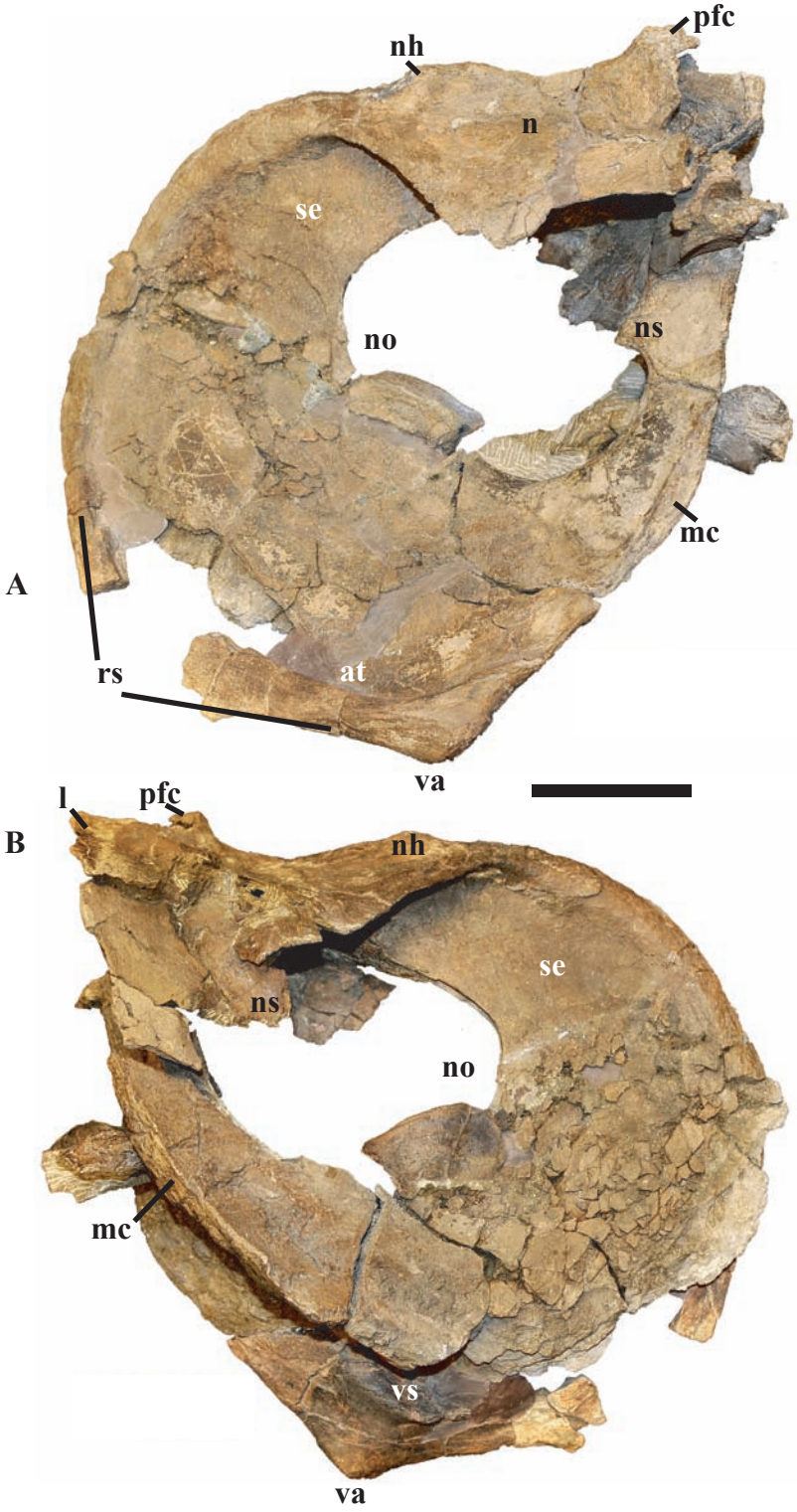

Figure 17. Photographs of the holotype premaxillae. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 16800. **A**, left lateral view; **B**, right lateral view. **Abbreviations**: **at**, anteroventral trough; **l**, lacrimal; **lc**, lacrimal contact; **mc**, maxillary contact; **n**, nasal; **nh**, nasal horncore; **no**; narial opening; **ns**, narial spine; **pfc**, prefrontal contact; **rs**, rostral scar; **se**, septum; **va**, ventral angle; **vs**, ventral shelf. Scale bar = 10 cm.

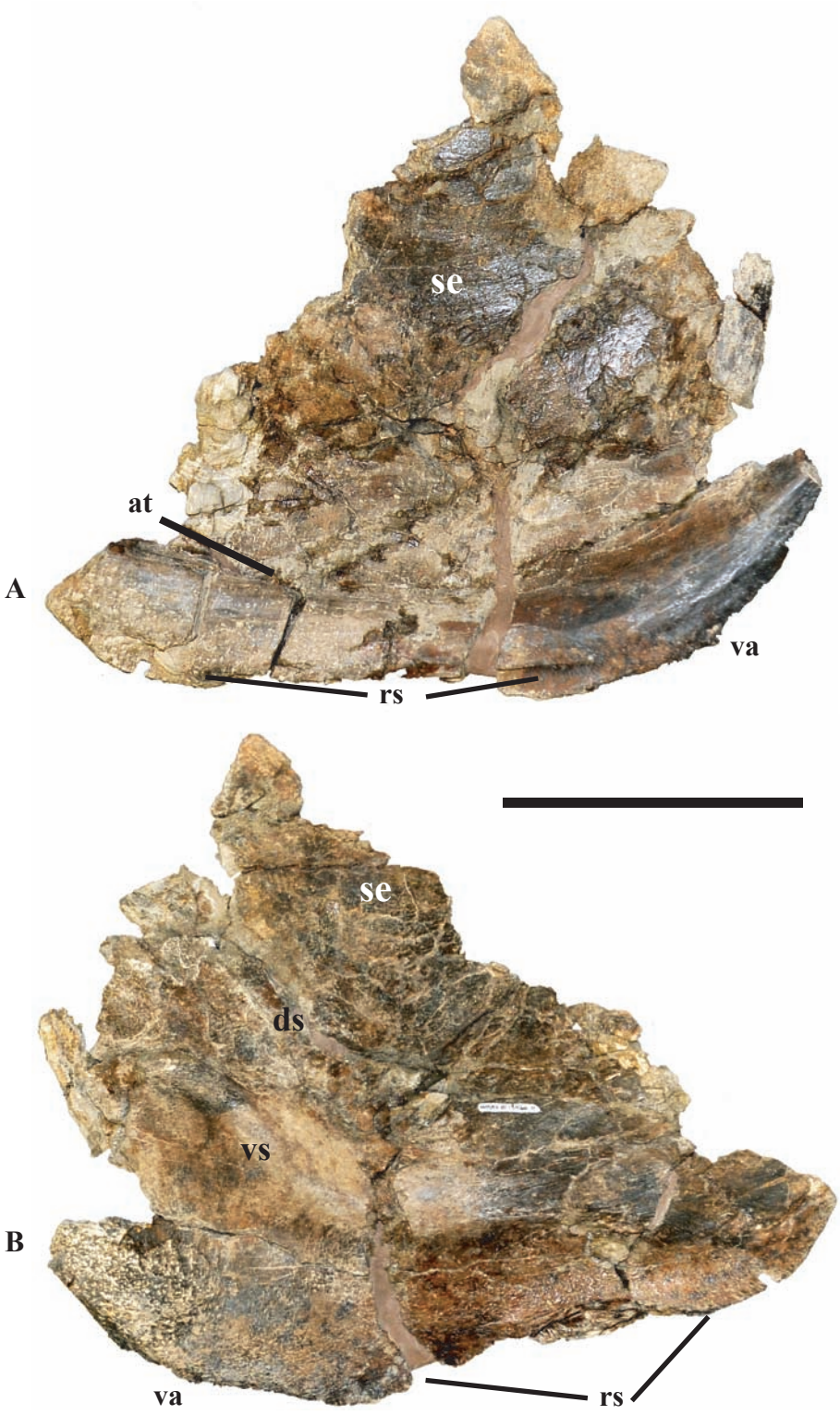

Figure 18. Photographs of the referred left premaxilla. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 19466.4. **A**, Lateral view; **B**, Medial view. **Abbreviations**: **at**, anteroventral trough; **ds**, dorsal shelf; **rs**, rostral scar; **se**, septum; **va**, ventral angle; **vs**, ventral shelf. Scale bar = 10 cm.

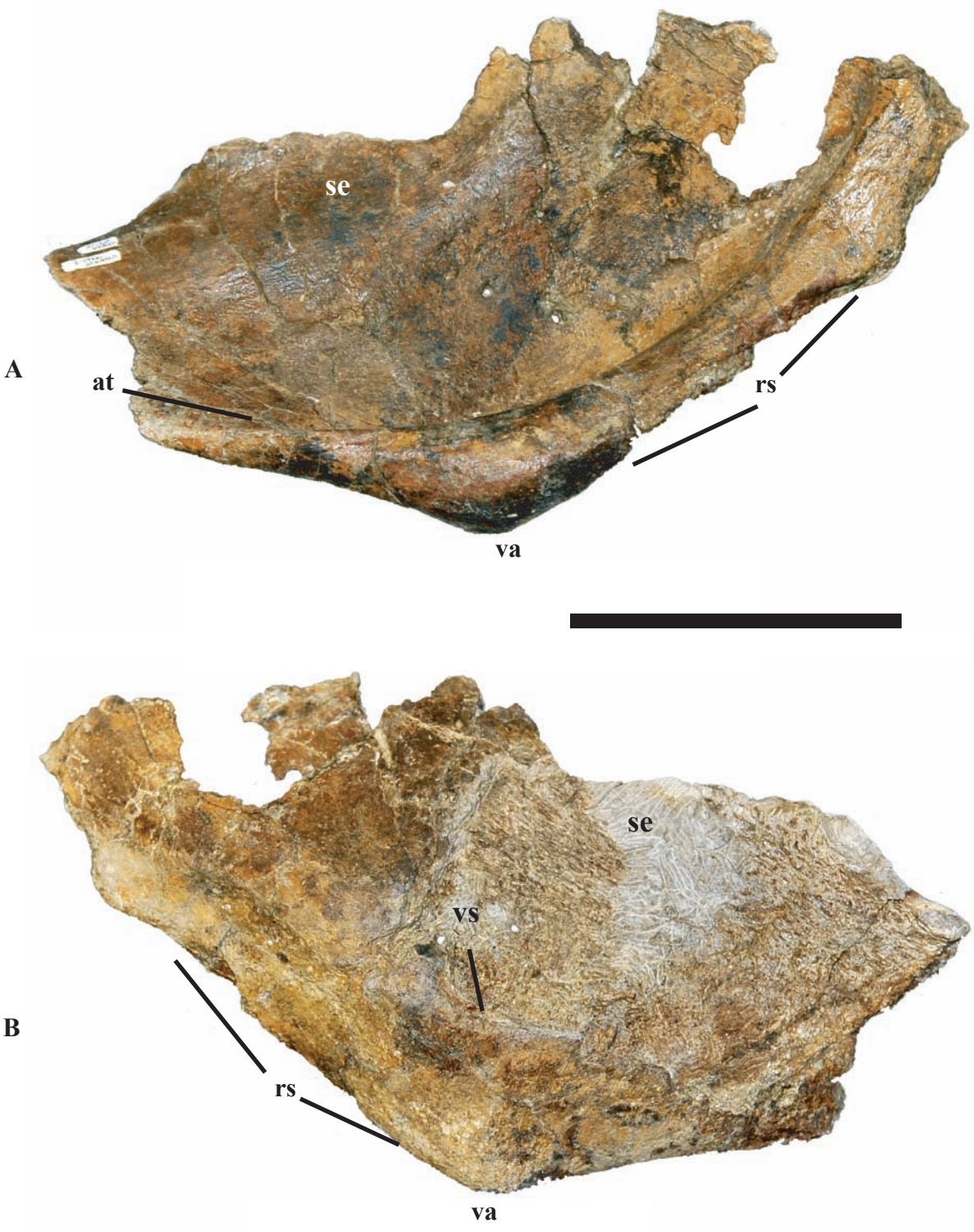

Figure 19. Photographs of the referred right premaxilla. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 19466.3. **A**, lateral view; **B**, medial view. **Abbreviations**: **at**, anteroventral trough; **rs**, rostral scar; **se**,septum; **va**, ventral angle; **vs**, ventral shelf. Scale bar = 10 cm.

Diabloceratops (UMNH VP 16699), although it was not described by Kirkland and DeBlieux (in press).

The rostral portion of the premaxilla is deep, forming a thin, rounded, median premaxillary septum within the narial fossa that extends between the endonaris and the ectonaris. In part because of the dorsal expansion of the narial region, the premaxillary septum appears to be more extensive than in all other known ceratopsids. Rostrally, the nasals contribute to the premaxillary septum, with the premaxillae slotting into the bifurcated rostral processes of the nasals (Fig. 15). In contrast to the typical centrosaurine condition, however, the premaxillary septum of *Nasutuceratops* extends caudally to underlie the nasal horncore. Extending into and possibly well beyond the endonaris, the premaxillae possesses a robust, caudodorsally directed process that is a caudal continuation of the premaxillary septum. Unlike the chasmosaurine condition, the premaxillary septum lacks a narial strut or any secondary foramina or depressions (Lehman, 1990; Sampson, 1995; Kirkland and DeBlieux, in press). The premaxillary septum is poorly preserved in the *Nasutuceratops* holotype, preventing observation of surface features such as ectonarial sulci that have been described for other centrosaurines (Sampson, 1995; Penkalski and Dodson, 1999; Kirkland and DeBlieux, in press; Sampson et al., in prep). The endonaris is relatively small and elliptical as viewed laterally. It is located in the caudodorsal portion of the premaxillae, bordered rostrally by the premaxillry septum, caudally by the ascending maxillary process, and dorsally by the nasals.

Both premaxillae preserved in UMNH VP 16800 exhibit an unusual caudoventral process that ascends dorsally more than in any other ceratopsid, approaching the dorsal

margin of the skull (Fig. 15). In this conformation, *Nasutuceratops* closely resembles the condition present in basal neoceratopsians (e.g., *Protoceratops*, AMNH 6444; You and Dodson, 2004). This feature is thus regarded as symplesiomorphic in the Utah taxon. The rostrodorsal extent of the maxillary process contributes in part to the narial spine, as evidenced by the corresponding suture, which extends the length of the rostrodorsal margin of the process. In contrast to the typical centrosaurine state, the ascending maxillary process does not appear to contact the lacrimal; however, this inference cannot be confirmed because the necessary morphology is not well preserved in the holotype specimen. The left premaxilla of UMNH VP 16800 possesses an inclined, beveled ventral edge that is the caudal continuation of the rostral cutting edge, terminating in a robust ventral angle. In profile, the ventral angle drops well below the ventral margin of maxillary tooth row (Fig. 13). In contrast to more basal (nonceratopsid) neoceratopsians (e.g., *Magnirostris*, IVPP V 12513; *Bagaceratops*, ZPAL MgD-I/126) and the centrosaurine *Diabloceratops* (Maryanska and Osmólska, 1975; You and Dong, 2003; Kirkland and DeBlieux, in press), *Nasutuceratops* does not appear to possess an accessory antorbital fenestra.

Medially, a narrow ventromedial shelf abuts the premaxillary flange of the maxilla, forming a short hard palate (Fig. 17). This feature is preserved on the left premaxilla of UMNH VP 16800 and otherwise appears to be present only in *Pachyrhinosaurus* (TMP 1986.55.153) among centrosaurines (Sampson, 1995; Currie et al., 2008).

Maxilla

Only the left maxilla is preserved with the holotype of *Nasutuceratops* (Fig. 20), but a nearly complete right maxilla (UMNH VP 19466.1) has been recovered from another locality (Fig. 21). The nearly complete and apparently undistorted holotype maxilla is roughly triangular. As viewed in a medial or lateral aspect, the element can be divided into a dorsal ascending ramus and a ventral horizontal ramus, with the latter being the caudal continuation of the tooth row. A dorsal branch of the dorsal ascending ramus possesses a thin-walled, well defined contact surface for the caudodorsal process of the premaxilla that extends the length of the ascending ramus. The premaxillary contact, which appears hypertrophied relative to that of other ceratopsids, is here considered an autapomorphy of *Nasutuceratops*; it is deeply excavated ventrally and shallows dorsally (Figs. 20, 21). As preserved, the lateral branch of the ascending ramus has a well developed contact surface for the jugal. As is typical of ceratopsids, the antorbital fenestra shows minimal development, situated in a deep, crescentic excavation between the two branches of the dorsal ascending ramus (Sampson, 1995; Kirkland and DeBlieux, in press).

Based on comparisons with the more complete specimen (UMNH VP 19466.1), approximately 40 mm of the ventral horizontal ramus is absent in the holotype maxilla. The holotype preserves 22 tooth positions and preserves 20 *in situ* teeth at various stages of wear and replacement. The more complete UMNH VP 19466.1 contains 29 alveoli, and this is the estimated total number of maxillary tooth positions. At present, it has not been ascertained whether the teeth are double-rooted, as in other ceratopsids, or single-rooted, as in more basal neoceratopsians. As is typical of ceratopsids, the lingual surfaces

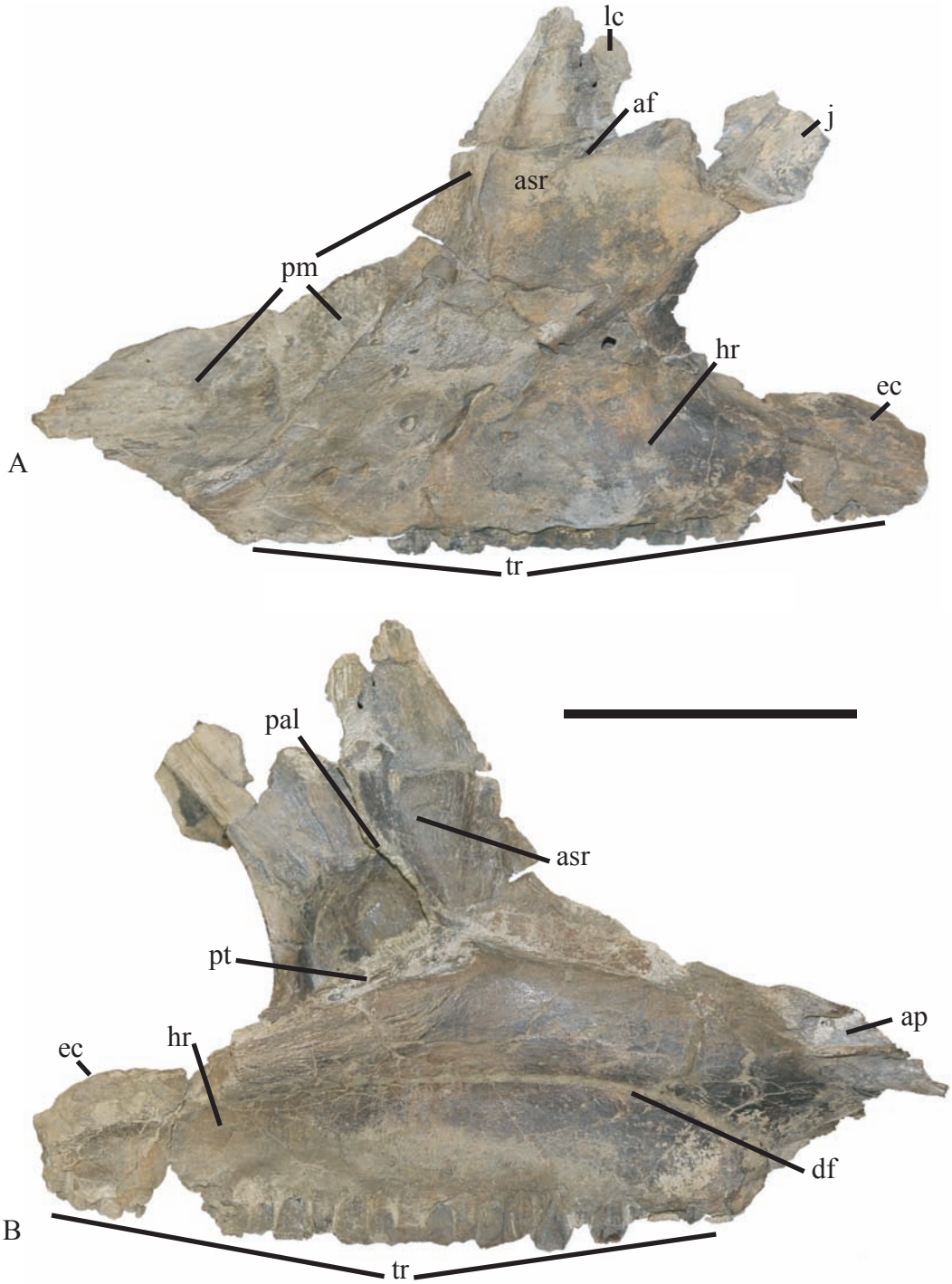

Figure 20. Photographs of the holotype left maxilla. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 16800. **A**, lateral view; **B**, medial view. **Abbreviations**: **af**, antorbital fenestra; **ap**, anterior process to slot into premaxilla; **asr**, ascending ramus; **df**, dental foramina; **ec**, ectoterygoid contact; **hr**, horizontal ramus; **j**, jugal contact; **lc**, lacrimal contact; **pal**, palatine contact; **pm**, premaxilla contact; **pt**, pterygoid contact; **tr**, tooth row. Scale bar = 10 cm.

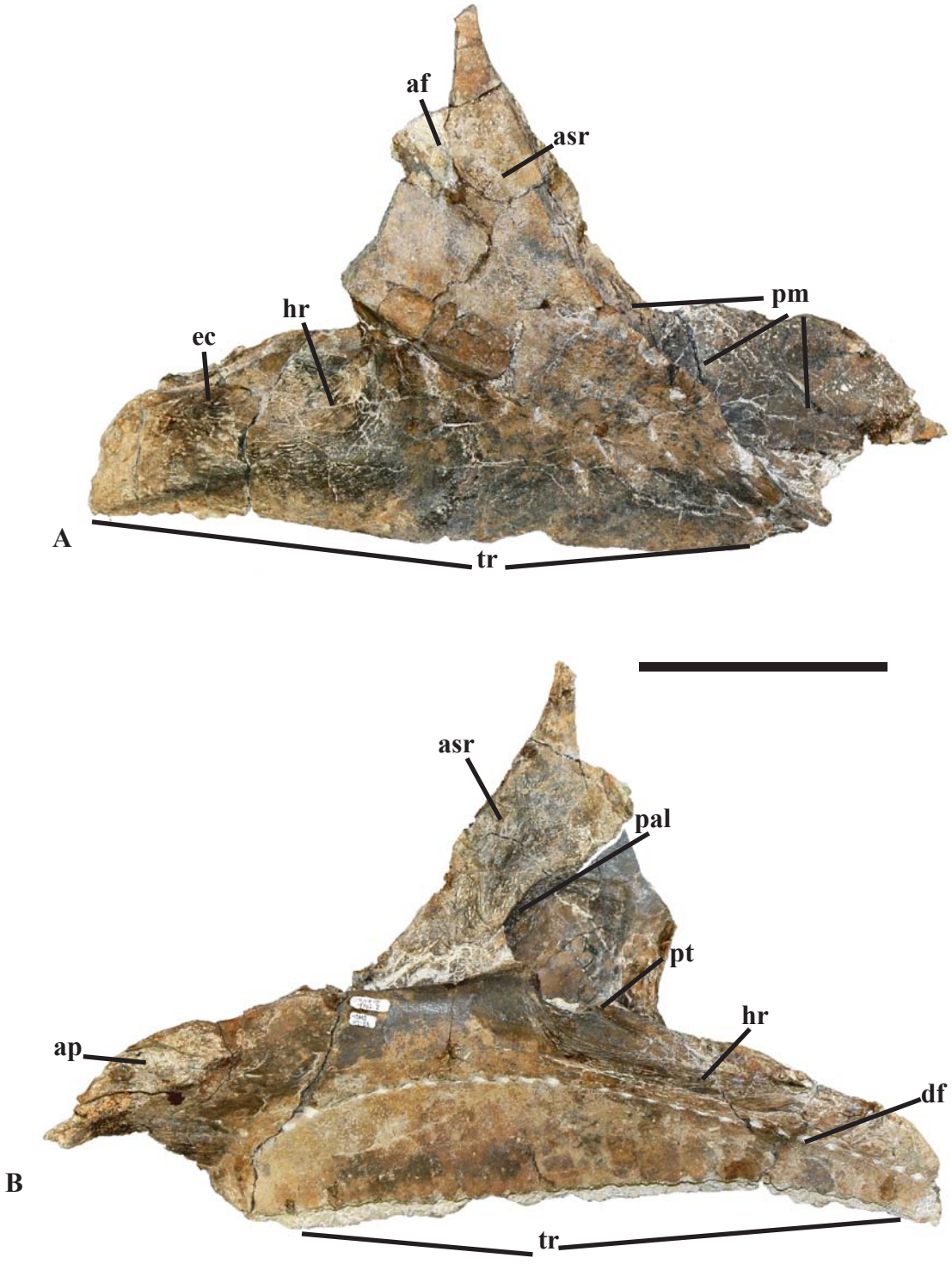

Figure 21. Photographs of the referred right maxilla. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 19466.2. **A**, lateral view, **B**, medial view. **Abbreviations**: **ap**, anterior process to slot into premaxilla; **asr**, ascending ramus, **df**, dental foramina; **ec**, ectoterygoid contact, **hr**, horizontal ramus; **j**, jugal contact; **pal**, palatine contact; **pm**, premaxilla contact; **pt**, pterygoid contact; **tr**, tooth row. Scale bar = 10 cm.

of the maxillary teeth show nearly vertical wear facets (Ryan, 2007; Kirkland and DeBlieux, in press).

UMNH VP 19466.1 preserves the entire ventral horizontal ramus, demonstrating that the caudalmost portion of this process forms a large, rounded shelf that includes contacts for pterygoid (medially) and the ectoterygoid (laterally). A similar conformation has been noted in basal neoceratopsians (e.g., *Protoceratops*, AMNH 6466; Brown and Schlaikier, 1940b; You and Dodson, 2004) and *Diabloceratops* (UMNH VP 16699; Kirkland and DeBlieux, in press), making the conformation of this character symplesiomorphic. The palatine contacts the internal surface of the maxilla along a well defined medial shelf that arches above the dental battery immediately rostral to the pterygoid. The rostral portion of the medial shelf is nearly horizontal, occurring well above (~80 mm) the dental battery, whereas the caudal portion curves distinctly ventrally. The contact for the pterygoid in UMNH VP 19466.1 is deeply excavated, forming a well defined trough. The pterygoid contact in the holotype maxilla is similarly well defined, but not as deeply excavated; however, this variation may be due at least in part to postmortem crushing and abrasion in this area.

Viewed caudally and medially, an elliptical, deeply excavated maxillary cavity is evident, formed medially by the maxilla, palatine, and pterygoid, and dorsally by the lacrimal, palatine, and maxilla. This cavity lies directly beneath the antorbital fenestra and occurs largely within the ventral portion of the dorsal ascending ramus. Rostrally, a medially directed flange of the maxilla with a double socket abuts its counterpart, slotting into the premaxilla to contribute to an abbreviated hard palate (Figs. 20, 21). The long axes of the sulci on this flange are oriented rostrocaudally (Fig. 22). The double faceted

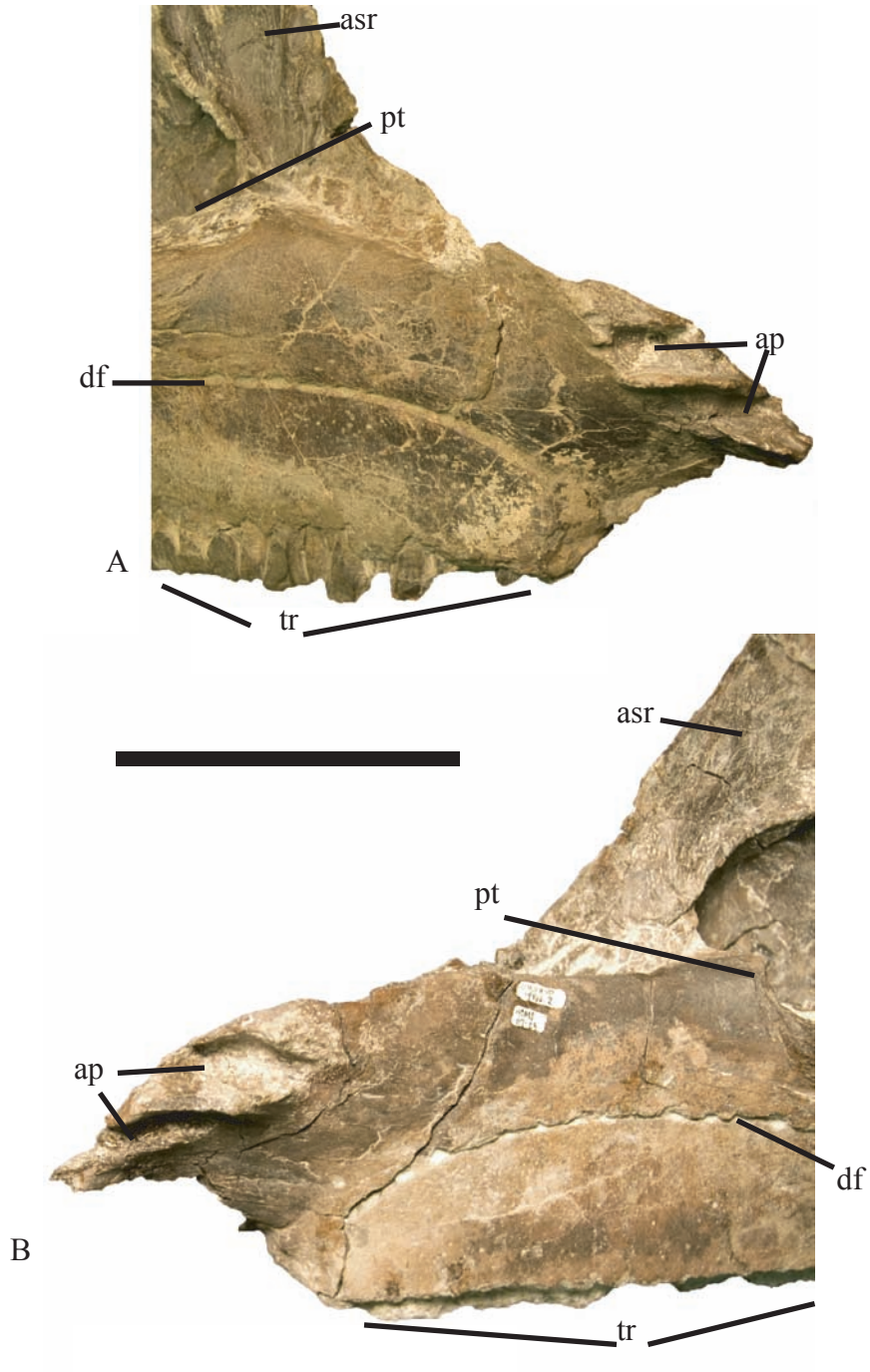

Figure 22. Photographs of the double faceted medial flange of the holotype and referred maxillae. *Nasutuceratops titusi* gen. et sp. nov. **A**. holotypemaxilla; **B,** referred maxilla**.** **Abbreviations**: **ap**, double faceted anterior process to slot into premaxilla; **asr**, ascending ramus; **df**, dental foramina; **pt**, pterygoid contact; **tr**, tooth row. Scale bar = 10 cm.

conformation of this flange is autapomorphic for *Nasutuceratops*.

Externally, the maxilla is perforated on both the dorsal ascending ramus and the ventral horizontal ramus by a variable number of irregularly placed and shaped foramina. The foramina are rostroventrally directed and likely transmitted neurovascular supply to the cheek region. As stated above, there is no evidence in either the premaxilla or the maxilla of an accessory antorbital fenestra. Caudally, the maxilla has a moderately well developed buccal excavation that appears less well defined than in other ceratopsids (Sampson, 1995; Ryan, 2007).

The maxilla of *Nasutuceratops* is distinguished from the typical ceratopsid morphology by several autapomorphies, including expanded premaxillary contact with deeply excavated sulcus; double faceted, medially directed flange that slots into premaxilla and contributes to hard palate; and elevated horizontal medial shelf (Figs. 20, 21). Additionally, the maxilla is distinguished from the typical ceratopsid condition in possessing a steeply angled dorsal ascending ramus, a symplesimorphic character observed in basal neoceratopsians (e.g., *Protoceratops*; AMNH 6414). The maxilla is further distinguished from the typical ceratopsid condition in that the entire tooth row is displaced ventrally (Figs. 13, 20, 21). This ventral displacement of the tooth row is similar to that seen in *Diabloceratops* (UMNH VP 16699) and *Avaceratops* (ANSP 15800), although this character has not previously been noted for either taxon (Penkalski and Dodson, 1999; Kirkland and DeBlieux, in press). This displacement of the tooth row in the Utah taxon (best preserved in UMNH VP 16800) differs slightly from that of *Diabloceratops* (UMNH VP 16699) in that, as viewed laterally, the latter taxon exhibits a greater external exposure of the maxilla rostral to the tooth row (Fig. 13). A ventrally

displaced maxillary tooth row also occurs in many basal neoceratopsians (e.g., *Bagaceratops*, ZPAL MgD-I/126, and *Protoceratops*, AMNH 6438) and is thus inferred here to be symplesiomorphic.

Nasals

The paired nasals of the holotype skull of *Nasutuceratops* (UMNH VP 16800) are nearly complete, preserving the full extent of the contact with the premaxillae (Fig. 15). A second disarticulated right nasal recovered from another quarry (UMNH VP 19466.1) exhibits similar morphology and is here referred to *Nasutuceratops*. The holotype nasals are completely fused along the midline, forming the rostrodorsal portion of the facial skeleton (Fig. 23). Rostrocaudally, the nasals are short (~ 248 mm in UMNH VP 16800) relative to other more derived centrosaurines, contacting the premaxillae rostrally and ventrally, the maxillae ventrally, and the lacrimals and prefrontals caudally. The extremely abbreviated nasal and maxilla result in an exceptionally short, tall preorbital facial skeleton relative to other centrosaurines, arguably the shortest known for any centrosaurine (Table 2).

The nasal horncore, positioned caudodorsal to the nasal opening, is low, long-based, and blade-like. It is pinched transversely along the caudal portion, with a slightly raised, tear-drop shaped rostral expansion formed in part by contributions from the premaxillae (Fig. 23). There is no evidence of an accessory epinasal ossification on the nasal horncore, as occurs in many chasmosaurines. The surface texture of the horncore in UMNH VP 16800 is moderately obscured due to surface weathering, but overall it appears typical of other ceratopsids, being highly rugose and vascularized. Rostroventral

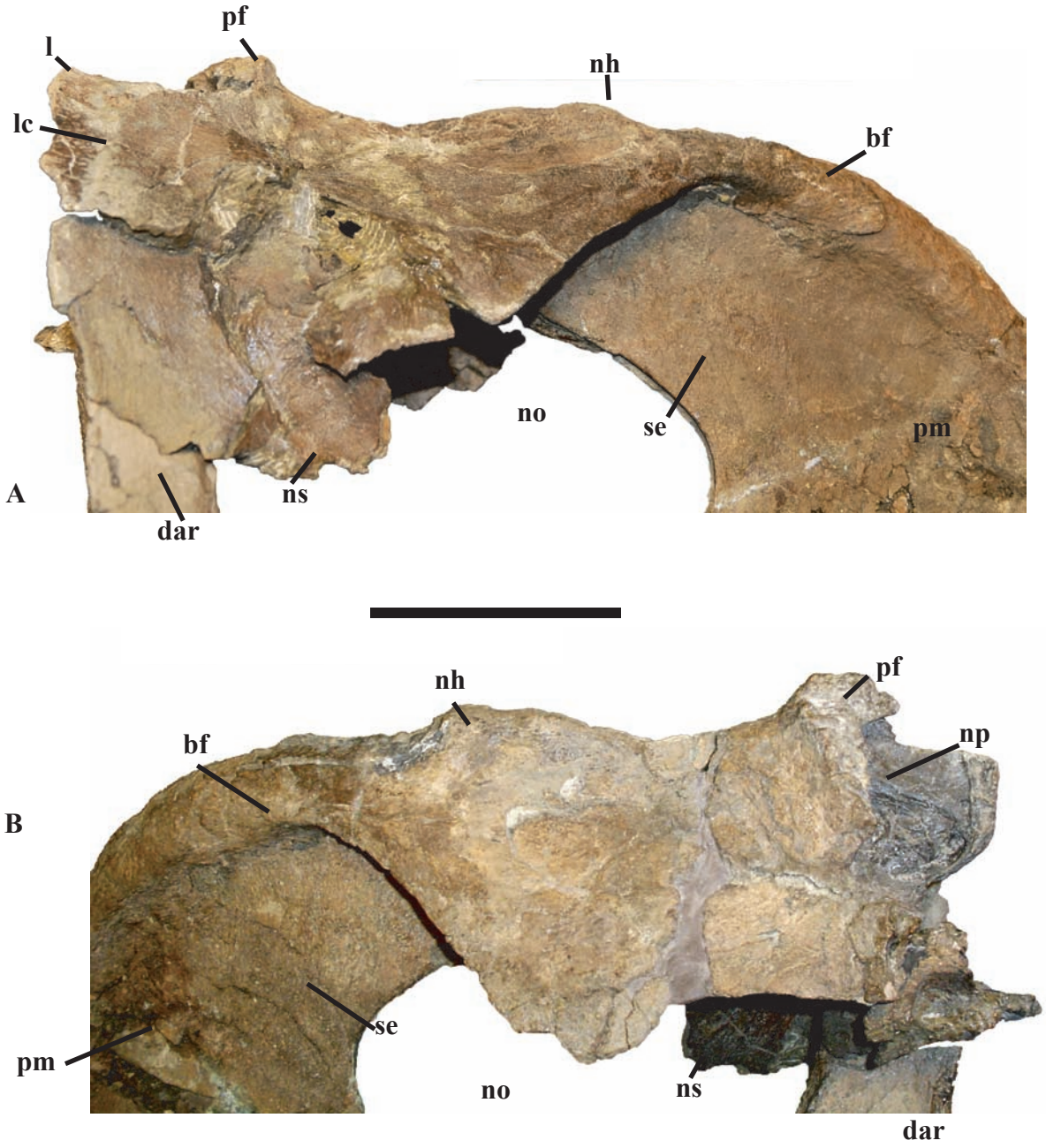

Figure 23. Photographs of the holotype nasals. *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 16800. **A**, right lateral view, **B**, left lateral view. **Abbreviations**: **bf**, bifurcated process to contact premaxilla; **dar**, dorsal ascending ramus of the premaxilla; **l**, lacrimal; **lc**, lacrimal contact; **nh**, nasal horncore; **no**; narial opening; **np**, nasal pnumatcity; **ns**, narial spine; **pf**, prefrontal; **pm**, premaxilla; **se**, septum. Scale bar = 10 cm.

Table 2 Measurements of maximum preorbital skull height (POH) and maximum preorbital skull length (POL) for select centrosaurine taxa, and the ratio of POL/POH.

TAXON	SPECIMEN	**POH** = Maximum Preorbital Skull Height (mm)	**POL** = Maximum Preorbital Skull Length (mm)	**POL/ POH**
Diabloceratops eatoni	UMNH VP 16699	260	400	1.54
Nasutuceratops titusi	UMNH VP 16800	450	410	1.09
Avaceratops lammersi	ANSP 15800	180*	280*	1.56*
Centrosaurus apertus	YPM 2015	350	580	1.66
Styracosaurus albertensis	NMC 344	300*	530	1.77*
Einiosaurus procurvicornis	MOR 456 8-9-6-1	280*	440*	1.57*
Achelousaurus horneri	MOR 485	275*	410*	1.49*
Pachyrhinosaurus lakustai	TMP 86.55.258	420	575*	1.37*

* = estimated

to the base of the horncore, the nasals protrude laterally and caudoventrally, forming much of the roof and the sides of the ectonarial fossa. These protruding sides are thin and blade-like along the ventral margin, thickening dorsally to form a hood that roofs over much of the endonaris (Fig. 23). Internally, the dorsal "roof" of the nasal cavity is similar to that observed in other centrosaurines (e.g., *Centrosaurus*, TMP 93.36.117; *Achelousaurus*, MOR 591). In contrast to more derived centrosaurines (e.g., *Centrosaurus*, *Styracosaurus*, *Achelousaurus*), however, the caudal portion of the nasals forms a deep, convex, saddle-shaped margin that contributes to a steeply inclined forehead (Figs. 13, 23). Similarly, caudal to the nasal horncore and ventral to the lacrimal and prefrontal contacts, the external surface of this nasal is deeply concave, forming bilateral symmetrical pneumatic excavations separated by a thin septum (Fig. 24).

The dorsal region of the nasal, including the lacrimal and prefrontal sutures, is well developed in the holotype specimen; however, the ventral portion has been obscured by predepositional breakage. The right premaxilla of the holotype is fused to a small piece of lacrimal. The prefrontal and lacrimal sutures are also well preserved in the referred nasal (UMNH VP 19466.1). The nasal-premaxilla contact resembles that of other centrosaurines, with the nasal bifurcating rostral to the nasal horncore to clasp the dorsal processes of the premaxillae (Lambe, 1904, 1913; Sternberg, 1950; Dodson, 1986; Sampson, 1995; Ryan, 2007; Ryan and Russell, 2007; Currie et al., 2008; Kirkland and DeBlieux, in press; McDonald and Horner, in press). A caudoventrally directed semicircular excavation leads into the nasal cavity at the junction of the nasal and premaxilla.

As is typical of centrosaurines, a narial spine is formed by contributions from both

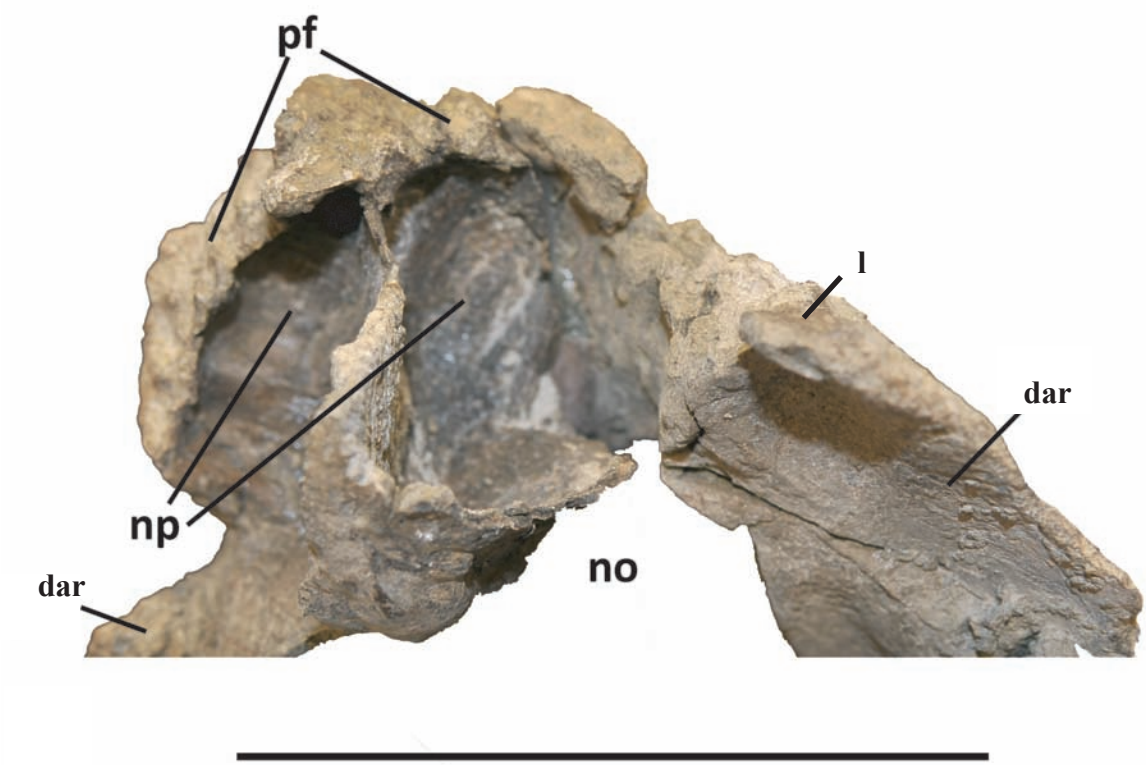

Figure 24. Photograph of the caudal margin of the holotype nasals in *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 16800, highlighting the autapomorphic nasal pnumaticity. **Abbreviations**: **dar**, dorsal ascending ramus of the premaxilla; **l**, lacrimal; **no**, narial opening; **np**, nasal pnumaticity; **pf**, prefrontal contact. Scale bar = 10 cm.

the nasal and premaxilla; this feature is deflected medially into the nasal cavity, resulting in a roughly hourglass-shaped opening into the nasal cavity proper as viewed rostrally (Sampson, 1995; Figs. 11, 18). Viewed laterally, the endonaris is relatively small and slightly crescentic, with a dorsally arched rostroventral border (Fig. 15). In lateral view, the nasal "hood" arches caudoventrally to become confluent with the narial spine protruding into the caudal portion of the ectonaris. The long axis of the endonaris is oriented almost horizontally, whereas it is subvertically oriented in most centrosaurines. The long axis of the endonaris is 160 mm long, comprising approximately 40% of the premaxillary facial skeleton.

In the second referred nasal (UMNH VP 19466.1), transverse and dorsoventral crushing of the nasal horncore suggests that this structure was hollow, presumably pneumatized by prefrontal-frontal pneumaticity extending rostrally into the nasals (Fig. 25). Pneumatic nasals are otherwise unknown in ceratopsians, and this feature is here regarded as autapomorphic for *Nasutuceratops*. Medially, the dorsal portion of the contact surface for the opposing nasal is rugose with rostrally arching ridges and troughs. The ventral portion of this contact is similarly rugose, but the ridges and troughs are more pronounced and oriented subhorizontally. Ventrally, a triangular excavation is present on the internal surface of the nasal immediately beneath the horncore, presumably related to the lateral and ventral extension of this element. Caudally, contacts with the lacrimal and prefrontal are well preserved. Medial and dorsal to the contact with the dorsal ascending process of the premaxilla are two ventral excavations, the smaller being triangular and the larger being more elliptical in shape.

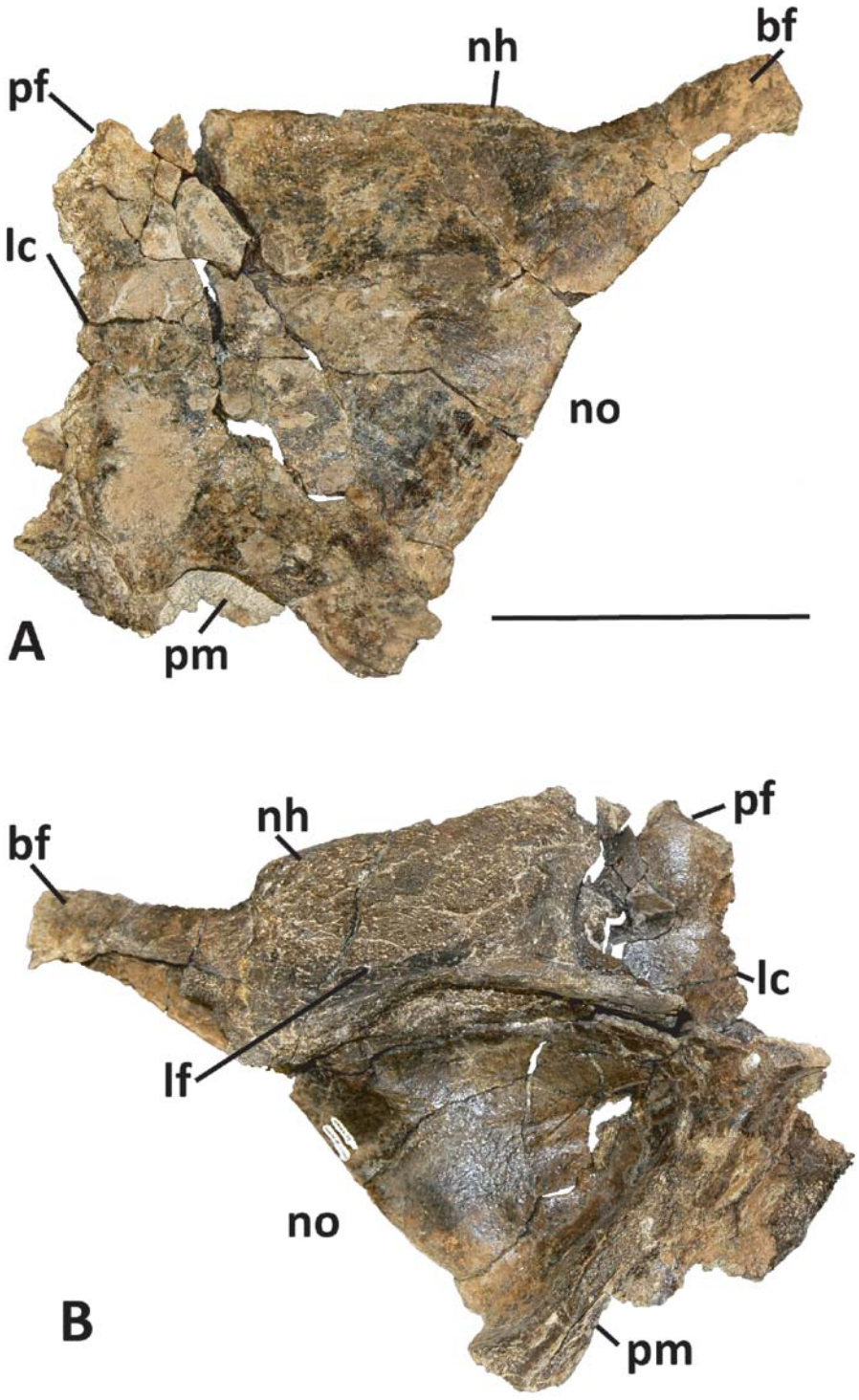

Figure 25. Photographs of the referred nasal of *Nasutuceratops titusi* gen. et sp. nov. UMNH VP 19466.4. **A**, lateral view, **B**, medial view. **Abbreviations**: **bf**, bifurcated process to contact premaxilla; **lc**, lacrimal contact; **lf**, line of fusion between the paired nasals; **nh**, nasal horncore; **no**, narial opening; **np**, nasal pnumaticity; **pf**, prefrontal contact; **pm**, premaxilla contact. Scale bar = 10 cm.

Circumorbital Regions

Postorbital

Along with the relatively short facial skeleton and dorsally expanded narial region, the most notable feature of *Nasutuceratops* is the supraorbital horncores (Fig. 13). As in all ceratopsids, the supraorbital horncores of the holotype occur as outgrowths of the postorbital and compose a major portion of this element, with a nominal contribution from the palpebral (Sampson et al., 1997). However, the supraorbital horncores of *Nasutuceratops* differ from those of all other ceratopsids in both orientation and, to a lesser extent, shape. The horncores show a strong curvature, with the bases directed rostrolaterally and the distal portions directed rostrally. The distal portion of the horncores also exhibits a pronounced torsional twist where the dorsal surface, at the midpoint of the horncore, rotates laterally. This torsional rotation produces a counterclockwise rotation at the distal tip of the left horncore and a clockwise rotation at the distal tip of the right horncore, as viewed from the horncore base (Fig. 13). In addition to their unusual orientation, these structures are also highly elongate (~457 mm in the holotype), exceeding relative and maximum supraorbital horncore length in any other centrosaurine (Table 3). Indeed, when viewed dorsally or laterally, the horncores extend rostrally almost to the tip of the snout, superficially resembling a "Texas-longhorn" bull. As is typical in ceratopsids, the horncores are subcircular in cross-section, tapering distally to a point, with numerous longitudinal ridges and grooves externally.

The supraorbital horncores in *Nasutuceratops* differ markedly from those of all other ceratopsids. Chasmosaurines tend to possess relatively elongate horncores in the supraorbital region, but without the strong rostral orientation or torsional twisting.

Table 3 Measurements of supraorbital horncore length and skull basal length for select centrosaurine taxa. *Nasutuceratops titusi* gen. et sp. nov. possesses the absolute longest supraorbital ornamentation of any centrosaurine.

TAXON	SPECIMEN	**SBL** = Skull Basal Length (mm)	**SHL** = Supraorbital Horncore Length (mm)
Diabloceratops eatoni	UMNH VP 16699	590	230
Albertaceratops nesmoi	TMP 2001.26.01	?	400
Nasutuceratops titusi	UMNH VP 16800	770	457
MOR Avaceratops	MOR 692	?	258
Centrosaurus apertus	ROM 767	677	100
Centrosaurus brinkmani	TMP 2002.68.05	530*	62
Styracosaurus albertensis	NMC 344	760*	60
Einiosaurus procurvicornis	MOR 456 8-9-6-1	670	85

* = estimated

Within Centrosaurinae, the great majority of taxa possess short supraorbital horncores (e.g., *Centrosaurus*, *Einiosaurus*) or pachyostotic bosses (*Achelousaurus*, *Pachyrhinosaurus*; Sampson, 1995). Only two centrosaurines, both basal forms, have been described with long supraorbital horncores—*Diabloceratops* and *Albertaceratops* (Ryan, 2007; Kirkland and DeBlieux, in press). *Zuniceratops*, *Diabloceratops*, and *Albertaceratops* possess supraorbital horncores similar to those of *Nasutuceratops* in being long and subcircular in cross-section, but these structures have a stronger dorsal (as opposed to rostral) component to their orientation and lack any evidence of a torsional twist. The supraorbital horncores in *Nasutuceratops* are situated rostrodorsal to the orbit, as in the centrosaurines *Diabloceratops* and *Albertaceratops*, as well as the chasmosaurines *Pentaceratops*, *Agujaceratops*, *Utahceratops*, and *Chasmosaurus*, but in contrast to the condition in other centrosaurines and chasmosaurines (Sampson et al., unpublished data).

The postorbital comprises a major portion of the caudal facial region, forming most of the dorsal margin of the orbit. Sutural contacts are with the lacrimal, palpebral, and prefrontal rostrally, the frontal medially, the parietal caudally, the squamosal caudolaterally, and the jugal ventrally; however, the contacts are mostly obscured in the preserved study sample due to a combination of fusion and breakage. The lacrimal and palpebral form most of the rostrodorsal and rostral margins of the orbit, respectively, whereas the ventral and caudal margins of the orbit are formed from the dorsal margin of the jugal. The nearly complete right orbit preserved on the holotype (UMNH VP 16800) indicates that *Nasutuceratops* possessed an elliptical orbit.

Medially, the postorbital of *Nasutuceratops* displays a smooth-walled cornual

sinus dorsal to the orbit that protrudes (106 mm) into the horncore shaft on UMNH VP 16800 (23% of the total horncore length). Since cornual sinuses are an internal feature, they are typically observed only on isolated postorbitals or fragmentary skulls. The holotype specimen of *Nasutuceratops* is broken in the orbital region, allowing this structure to be observed on both the right and left sides, although the morphology is better preserved on the left (Fig. 26). Like other ceratopsids with relatively elongate supraorbital horncores, (e.g., *Triceratops*), the cornual sinuses of *Nasutuceratops* occupy the center of the proximal horncore interior, in contrast to ceratopsids with relatively short supraorbital horncores, (e.g., *Centrosaurus*, *Anchiceratops*), in which the cornual sinus may occupy a position in the center or caudal to the center of the horncore (Farke, 2006).

The holotype (UMNH VP 16800) indicates that *Nasutuceratops* possesses a pronounced, vaulted skull roof in the interorbital region, formed largely by the prefrontals, frontals, palpebrals, and postorbitals. Together, these elements give the impression of the animal having a pronounced, rostrally facing forehead. A similar feature has been noted for *Diabloceratops* and *Albertaceratops*, as well as for several chasmosaurines (e.g., *Pentaceratops* and two undescribed taxa from the Kaiparowits Formation; Ryan, 2007; Kirkland and DeBlieux, in press; Sampson and Loewen, in press). The vaulted forehead spans the entire breadth of the skull and is laterally constrained by well developed antorbital buttresses. In *Nasutuceratops*, this character is only preserved on the right side of the holotype skull. Complete fusion of the bones forming the skull roof in this region (e.g., frontals and prefrontals) obscures all sutures; however, the prefrontals and frontals are presumed to have similar morphology to those

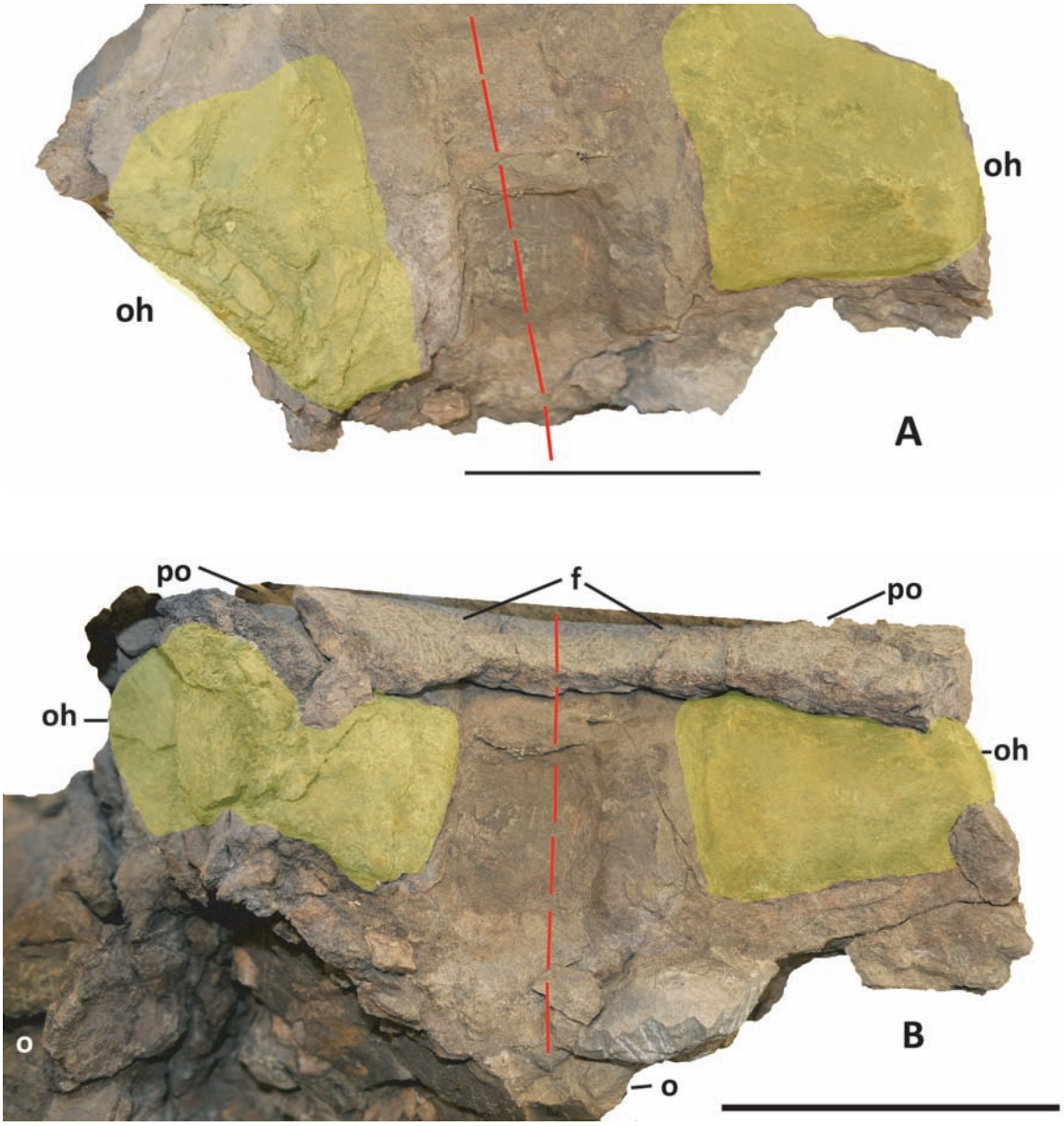

Figure 26. Photographs of the cornual sinuses (yellow) in the holotype skull, UMNH VP 16800, of *Nasutuceratops titusi* gen. et sp. nov. **A**, dorsal view with all surface bone removed, anterior is toward bottom of photograph. **B**, anterior view. Red dashed line is approximate midline of skull. **Abbreviations**: **f**, frontals; **po**, postorbital; **o**, orbital opening; **oh**, orbital horncore contact. Scale bars = 10 cm.

noted for other well-known centrosaurines (Sampson, 1995). As is typical of ceratopsids generally, the frontal forms the rostral-most margin of the frontal fontanelle, as well as a substantial portion of the supracranial cavity. Positioned medially and caudally to the postorbitals, the well-developed fontanelle forms an elongate oval with straight sides, a conforrmation typical of centrosaurines (Dodson et al., 2004).

Jugal

The holotype (UMNH VP 16800) preserves the dorsal margin of the right jugal, which forms the ventral and caudal margins of the right orbit, as well as a small (~ 50 mm) fragment of the dorsal margin of the left jugal (Fig. 27). The incomplete jugals are presumed to exhibit morphology typical of other centrosaurines (e.g., *Centrosaurus*, ROM 767; *Albertaceratops*, TMP 2001.26.1), contacting the lacrimal dorsally, the maxilla rostrally, the postorbital dorsocaudally, and the squamosal caudally. Dorsally, the jugal forms the thickened and rugose ventral margin of the orbit.

Epijugal

The ventral tip of the ceratopsid jugal is covered with an accessory ossification, the epijugal. A single disarticulated epijugal (UMNH VP 16800) is preserved with the holotype skull (Fig. 28). The epijugal is roughly trihedral in shape, possessing a flattened rostral surface and a deeply excavated rugose facet along the internal surface for articulation with the jugal and quadratojugal. Relative to other ceratopsids (e.g., *Centrosaurus*, AMNH 5239; *Styracosaurus*, TMP 2005.42.58), the epijugal is large—approximately 85 mm in length and 78 mm in width at the base—and represents the largest example known among centrosaurines. Compared to that of *Diabloceratops*

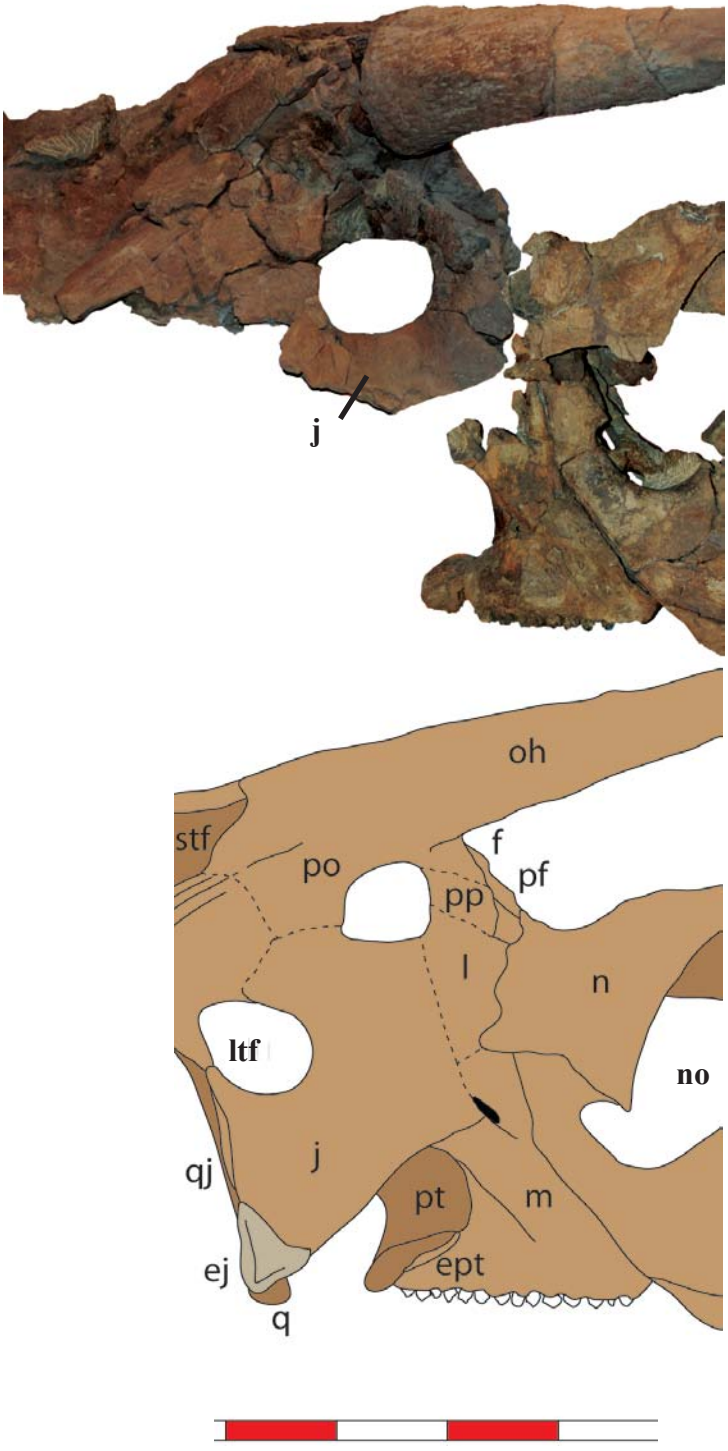

Figure 27. Photograph with reconstruction of the fragmentary holotype jugal. *Nasutuceratops titusi* gen. et sp. nov., UMNH VP 16800. **Abbreviations**:**ej**, epijugal; **ept**, ectoterygoid; **f**, frontal, **j**, jugal; **l**, lacrimal; **ltf**, lateral temporal fenestra; **m**, maxilla; **n**, nasal; **no**, narial opening; **oh**, orbital horn; **pf**, prefrontal; **po**, post orbital; **pp**, palpebral; **pm**, premaxilla; **pt**, pterygoid;**q**, quadrate; **qj**, quadratojugal; **stf**, supratemporal fenestra. Scale bar = 40 cm.

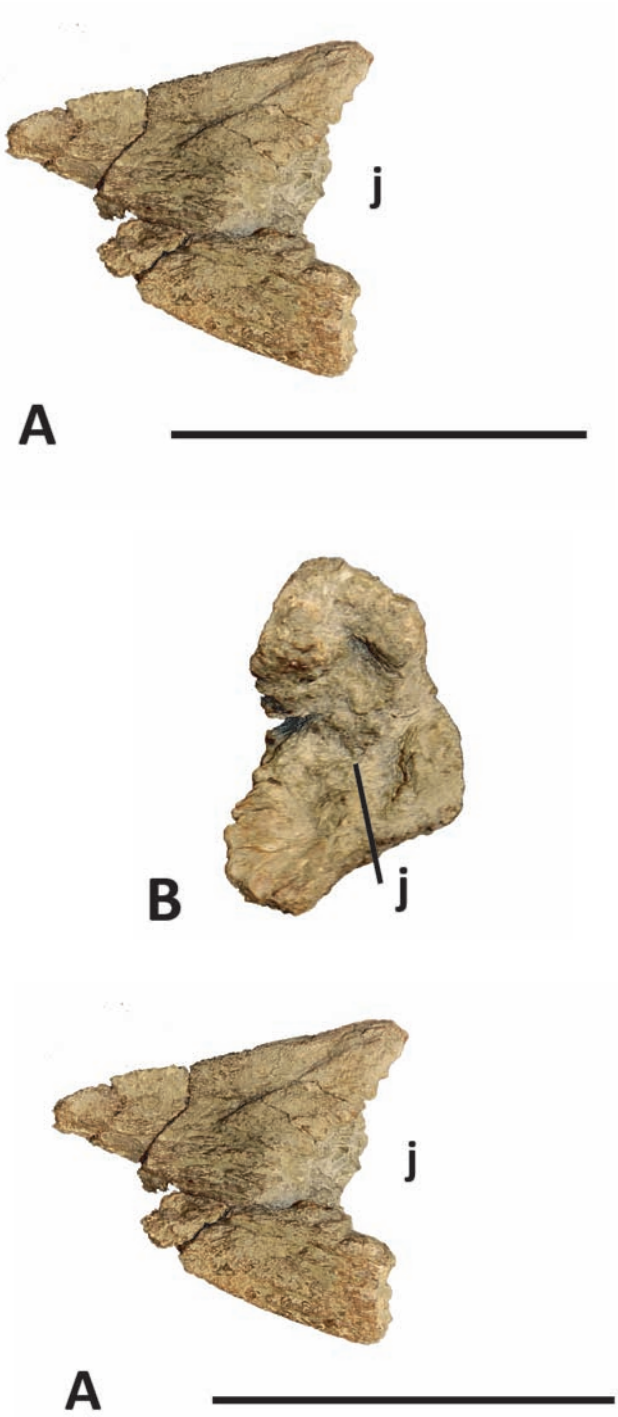

Figure 28. Photographs of the holotype epijugal UMNH VP 16800. **A**, anterior view; **B**, medial view; **C**, posterior view. **Abbreviations**: **j**, jugal/quadratojugal contact. Scale bars = 10 cm.

(UMNH VP 16699), the epijugal is similar in being large with a flattened rostral surface, but it is distinctly different in being much more angular and trihedral in shape. Large epijugals are more typical of chasmosaurines, and they may well be a basal feature of Ceratopsidae. Similar to other epiossifications found in ceratopsids, the external surface is highly vascularized and rugose, and likely bore a keratinous sheath during life.

Quadratojugal

A partial, disarticulated right quadratojugal (UMNH VP 16800), damaged along its dorsal and rostral edges, is preserved with the holotype specimen (Fig. 29). The quadratojugal closely resembles that described for other ceratopsids, being thin rostrally, and thick caudally, with an overall wedge-shape and well developed, rugose articulation facets along the rostral and medial surfaces for contacting the jugal (rostral), epijugal (medial) and quadrate (medial). The contact facet along the rostral surface is slightly concave and scored by a series of rugose grooves and ridges that accommodate the jugal. The thickened caudoventral portion possesses a raised, rugose, semirounded peak that lies between the jugal and quadrate and supports the caudal margin of the epijugal. Medial to this raised peak, the quadratojugal possesses a well defined excavation for the articulation with the quadrate.

Parietosquamosal Frill

As in other ceratopsids, the frill is formed from the fused parietals and paired squamosals. Unfortunately, the squamosals are only partially preserved in the holotype (UMNH VP 16800); however, the entire midline parietal bar and much of the transverse

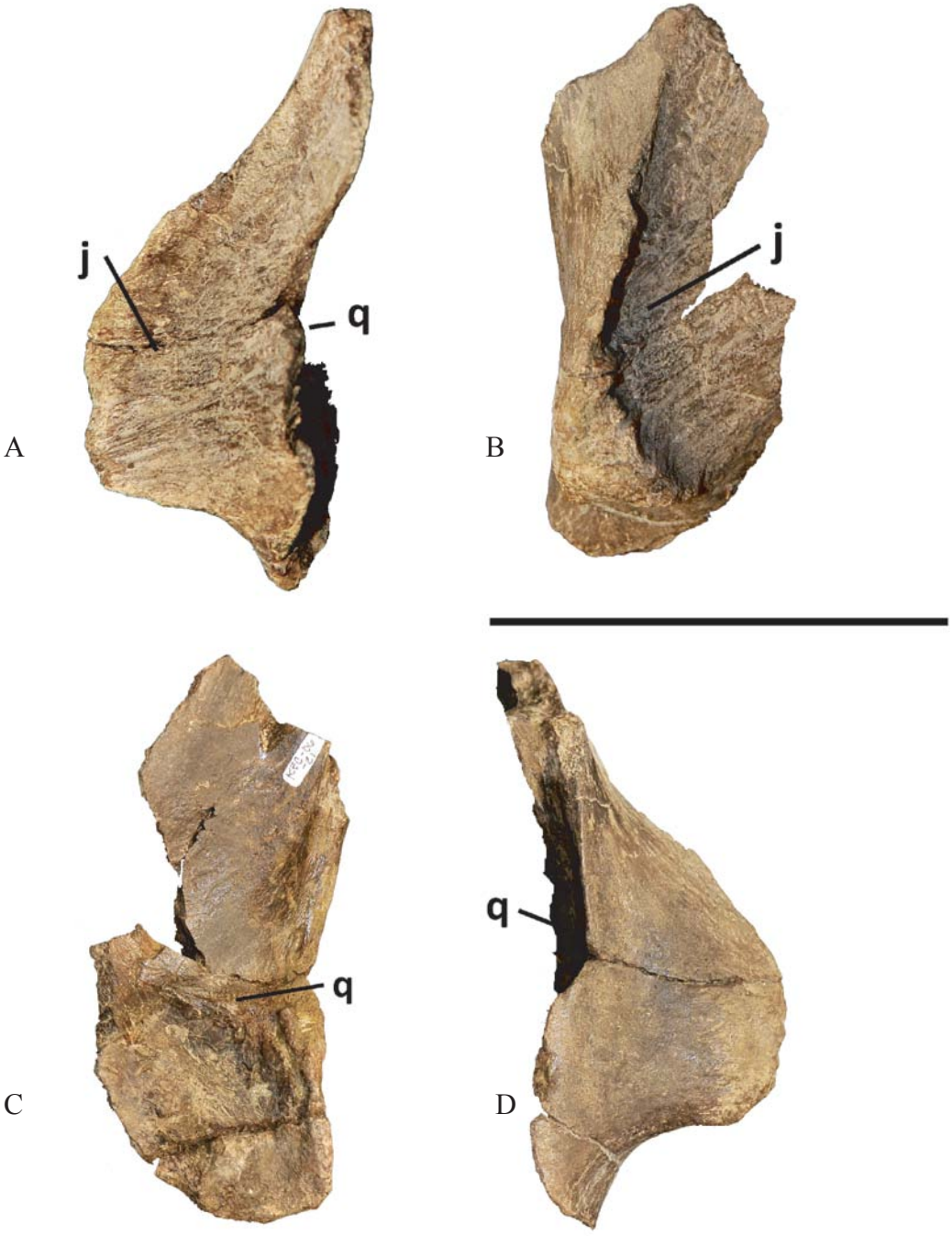

Figure 29. Photographs of the holotype quadratojugal UMNH VP 16800. **A**, anterior view; **B**, lateral view; **C**, medial view; **D**, posterior view. **Abbreviations**: **j**, jugal contact **q**, quadrate contact. Scale bar = 10 cm.

parietal bar are present. The frill is subrectangular in overall conformation, with the widest point located caudally (Fig. 30). Total frill length in UMNH VP 16800 is approximately 610 mm, and total width is estimated at 800 mm. Rostrocaudally, frill length is approximately equal to basal skull length. In overall shape, the parietosquamosal frill of *Nasutuceratops* resembles that of *Centrosaurus* (ROM 767), *Achelousaurus* (MOR 485) and *Einiosaurus* (MOR 456 8-9-6-1), although it differs greatly in morphology of the episquamosals and epiparietals (see below). As is typical of centrosaurines, the frill is perforated by large, oval fenestrae, one on either side of the midline, contained entirely within the boundary of the parietal. The long axis of each parietal fenestra is oriented rostrocaudally and is approximately 350 mm long in the holotype, comprising 57 % of total frill length. The transverse axis is approximately 260 mm in maximum width, comprising 33% of the total frill width. The frill is typical of centrosaurines in being generally saddle-shaped, with the dorsal surface convex transversely and concave rostrocaudally (Fig. 31).

Squamosal

Only a small portion of the left and right squamosals are preserved on the holotype skull (UMNH VP 16800), in particular the rostral most portions associated with the postorbital contact (Fig. 13). This specimen is augmented by a second referred squamosal (UMNH VP 19469), an isolated example also found in the lower portion of the middle unit of the Kaiparowits Formation of GSENM (Fig. 32). Referral of the latter to *Nasutuceratops* is based on overall conformation, including the presence of a pronounced, rostrocaudally directed transverse ridge. The referred right squamosal

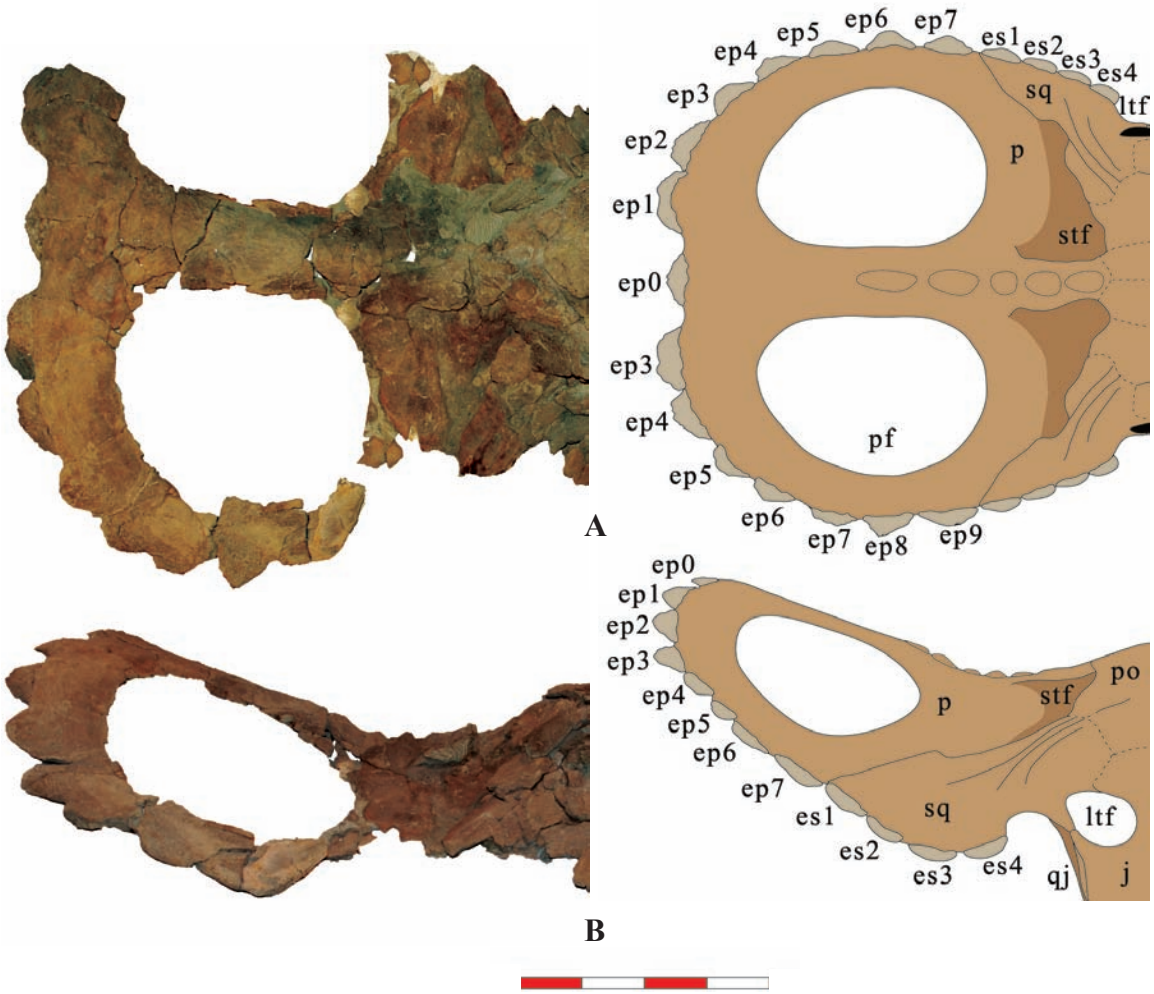

Figure 30. Photograph with reconstruction of the parietosquamosal frill, UMNH VP 16800. **A**. dorsal view; **B**, lateral view. **Abbreviations**: **ep**, epiparietal; **es**, episquamosal; **j**, jugal; **ltf**, lateral temporal fenestra; **p**, parietal; **pf**, parietal fenestra; **po**, postorbital; **qj**, quadratojugal; **sq**, squamosal; **stf**, supratemporal fenestra. Scale bar = 40 cm.

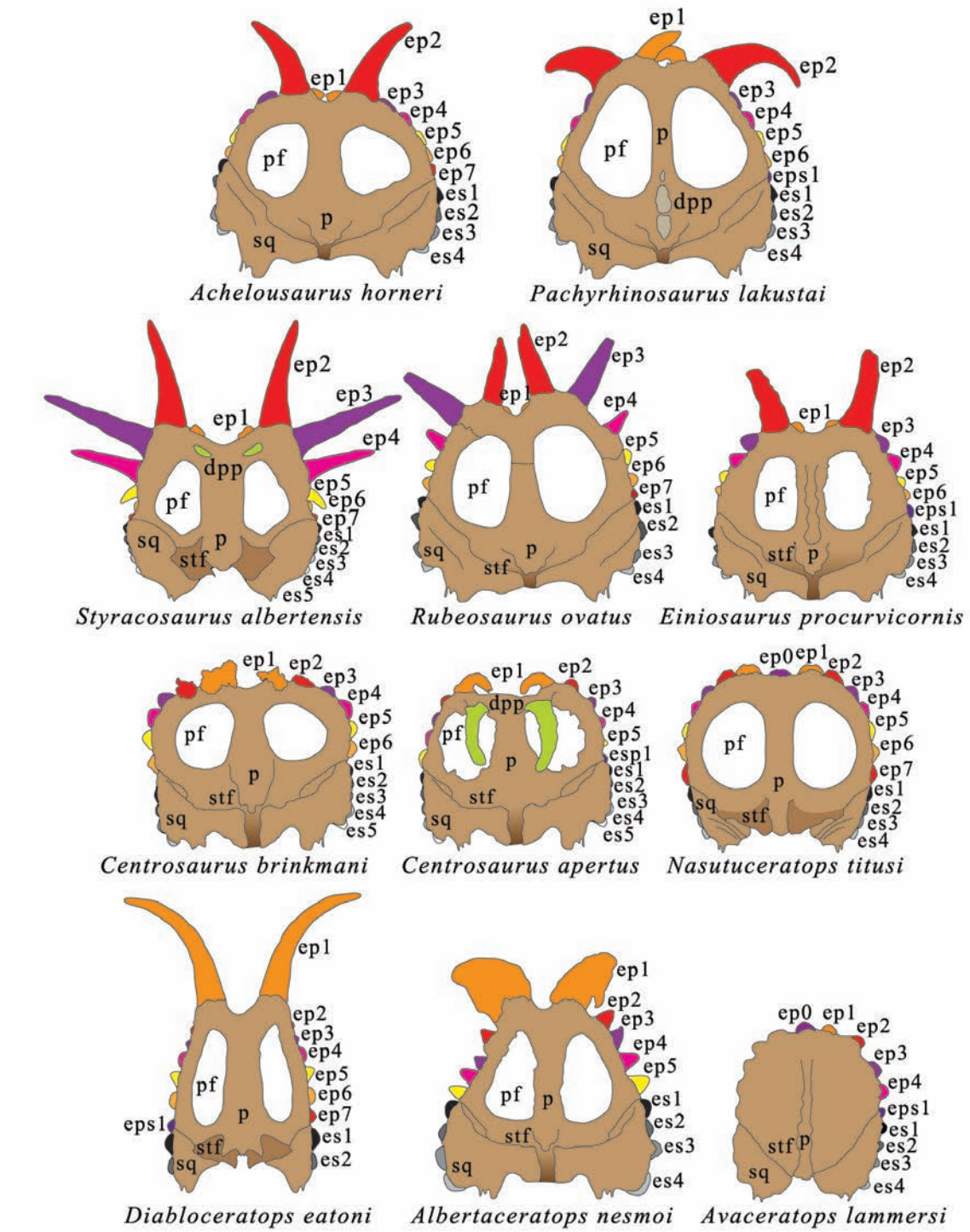

Figure 31. Diversity of parietosquamosal frills in select centrosaurine ceratopsids. Colors highlight homologous episossifications. **Abbreviations**: **ep**, epiparietal; **eps**, epiparietal-squamosal; **es**, episquamosal; **dpp**, dorsal parietal process; **p**, parietal; **pf**, parietal fenestra; **sq**, squamosal; **stf**, supratemporal fenestra (after Clayton et al., 2009).

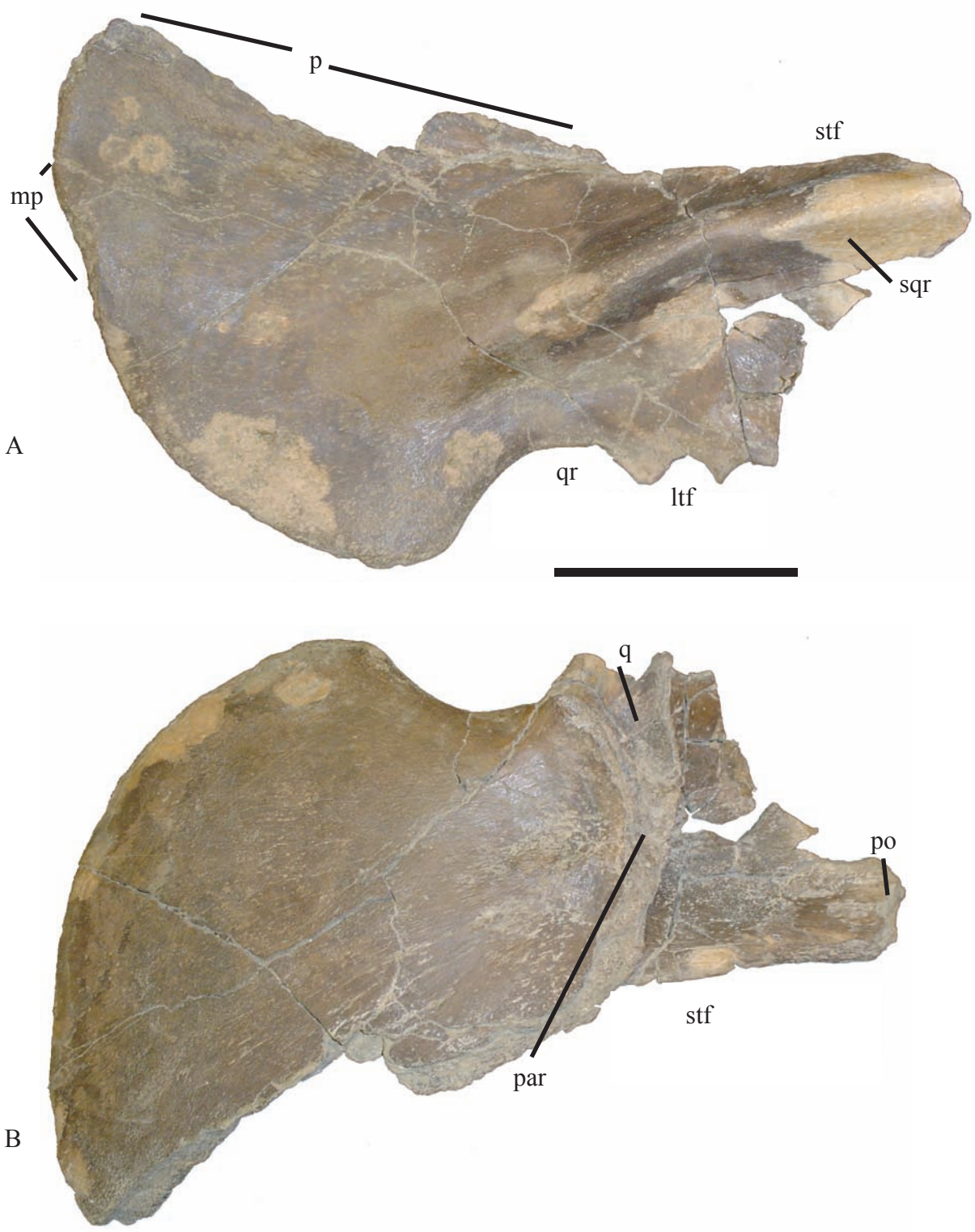

Figure 32. Photographs of the referred squamosal UMNH VP 19469. **A**, dorsal view; **B**, ventral view. **Abbreviations**: **j**, jugal contact; **ltf**, lateral temporal fenestra; **mp**, marginal processes; **p**, parietal contact; **par**, paroccipital contact; **po**, postorbital contact; **q**, quadrate contact; **qr**, quadrate ramus; **sqr**, squamosal ridge; **stf**, supratemporal fenestra. Scale bar = 10 cm.

(UMNH VP 19469), apparently from a subadult individual based on bone surface texture (Sampson et al., 1997), possesses the complete transverse ridge noted above. This transverse squamosal ridge is similar to that observed on an undescribed, isolated squamosal (NMMNH P34906) from the Fort Crittenden Formation of Arizona (Fig. 33). Unlike previously described squamosals pertaining to juvenile centrosaurines (e.g., *Einiosaurus*, MOR 456-8-13-7-9, Sampson, 1995), UMNH VP 19469 exhibits a strong rostrocaudal dorsal curvature. Otherwise, this specimen is relatively robust and characteristically centrosaurine, being rostrocaudally short and subrectangular, with a slightly undulating, fan-shaped caudolateral margin and a stepped rostromedial margin that represents the dorsal continuation of the quadrate groove (Dodson et al., 2004).

Although incompletely preserved in the holotype, a portion of the aforementioned squamosal ridge is preserved from the right side of the skull. The apex of this ridge preserved on the *Nasutuceratops* holotype is striated and rugose in texture, possessing two flat surfaces, one along the medial side and the other along the ventral side, which are presumed to be contact facets, but for which cranial elements are uncertain due to the fragmentary nature of the material (Fig. 34). In most respects, the squamosal of *Nasutuceratops* is typical of other centrosaurines, being squared off rostromedially and sharing an overlapping joint with the caudal postorbital. Rostromedially, the squamosal also contributes to the roof of the supratemporal fenestra, as in other ceratopsids. Although surrounding contacts are incompletely preserved in the holotype specimen, and therefore not directly observable, it is presumed that the squamosal of this taxon resembled that of other ceratopsids, contacting the jugal and postorbital rostromedially, parietal medially and caudally, quadratojugal rostromedially, and the quadrate and

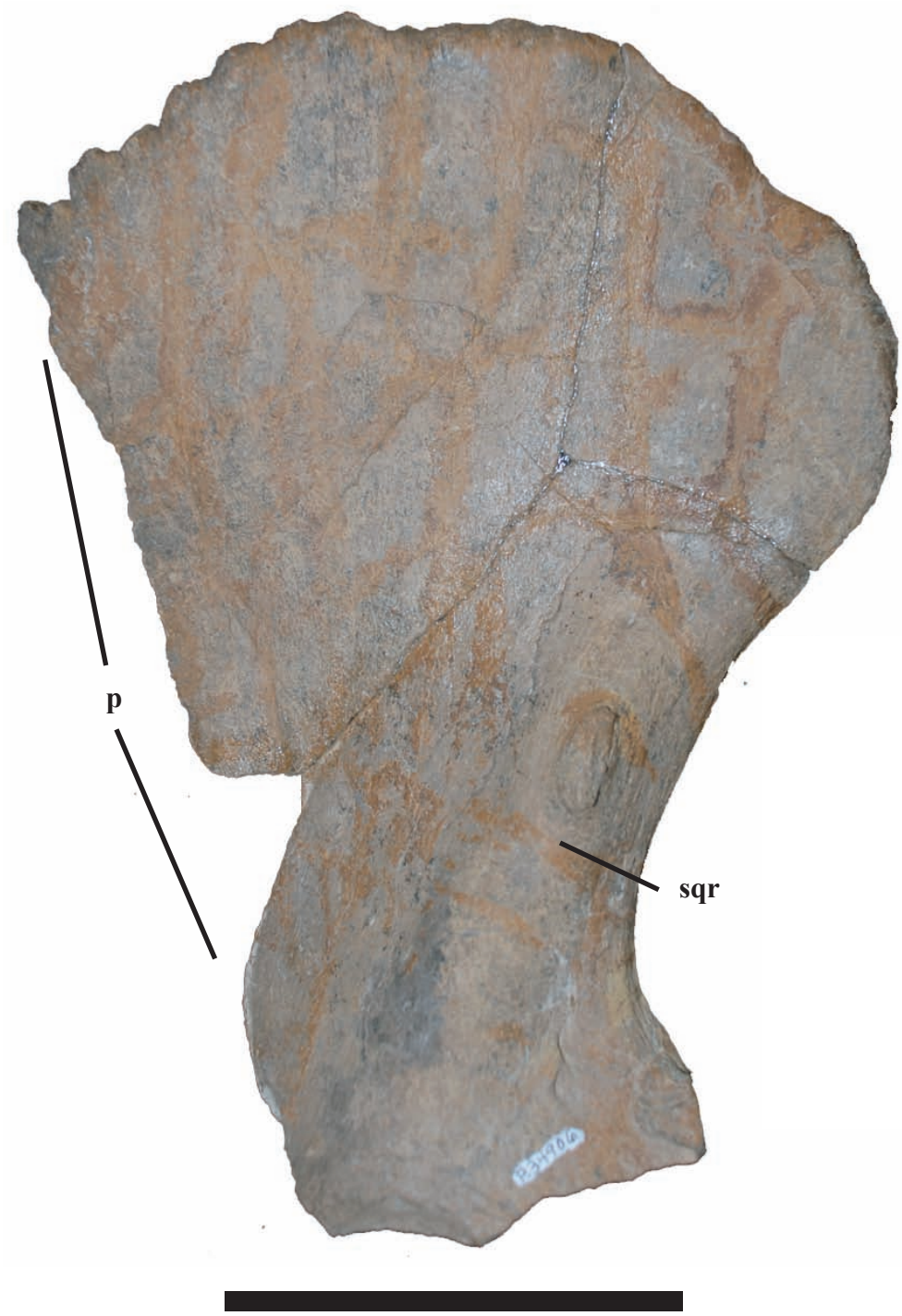

Figure 33. Photograph of an undescribed squamosal from Fort Crittenden Formation NMMNH P34906 in dorsal view, which shows a squamosal ridge similar to *Nasutuceratops titusi.* **Abbreviations**: **p**, parietal contact; **sqr**, squamosal ridge. Scale bar = 10 cm.

paroccipital process rostroventrally.

The squamosal abuts the parietal caudomedially, forming approximately one-half of the parietosquamosal frill. The squamosal can be subdivided into two halves as viewed dorsally: a convex rostromedial half supporting the highly pronounced transverse ridge and a protruding quadrate ramus (almost absent in UMNH VP 19469); and a broad, fan-shaped, concave caudolateral half. Although most of the quadrate ramus in UMNH VP 19469 has been lost to erosion, the morphology of the jugal notch is preserved, and appears similar to that of other centrosaurines. The pronounced transverse ridge in the juvenile squamosal has two, almost undulating protuberances along the apex of the ridge (Fig. 34).

The isolated referred squamosal (UMNH VP 19469) lacks episquamosals, but does possess four to five marginal undulations. It is presumed that, as in other centrosaurines, the squamosal of *Nasutuceratops* did have epiossifications attached to these undulations (Fig. 32). Additionally, the morphology of the episquamosals is presumed to closely match that of the parietal due to the relatively uniform conformation of epiossifications preserved on the parietal (see below). The presence of an epiossification across the squamosal-parietal contact cannot be determined on UMNH VP 19469 because of breakage to the caudolateral margin of the element. The stepped rostromedial margin is associated with the quadrate groove and forms the rostrolateral margin of the dorsotemporal fenestra, with the parietal forming the remainder of the fenestra. Although the rostrolateral portions of both the holotype and the referred squamosal have been lost to erosion, it is presumed that the rostrally projecting quadrate ramus contributed to the margin of the laterotemporal fenestra, as is typical of other

Figure 34. Photographs of the dorsal squamosal ridge in the holotype UMNH VP 16800. **A**, dorsal view; **B**, medial view; **C**, lateral view. **Abbreviations**: **cf**, contact facet. Scale bar = 10 cm.

ceratopsids. As in centrosaurines generally, the ventral surface includes a pronounced groove for the quadrate and an adjacent one for the paroccipital process of the exoccipital. These grooves are lined with a series of interfingering troughs, concave to semitriangular in cross-section. Slightly caudal to the quadrate slot are two shallow, subcircular depressions of uncertain function (Fig. 32).

Contrary to some previous claims (Dodson, 1990), the centrosaurine squamosal is highly conservative, showing minimal intracladal variation, thereby minimizing the role of this element for resolving within-group relationships (Sampson, 1995). The squamosal of *Nasutuceratops*, with its distinctive ridge on the dorsal surface, is unusual in this respect.

Parietal

The centrosaurine parietal forms approximately two-thirds of the parietosquamosal frill. The parietal contacts the squamosals rostrolaterally, the frontals and postorbitals rostrally, and the supraoccipital rostroventrally. In contrast to the taxonomic conservatism of the squamosal, the parietal of centrosaurines is typically unique at the species level, arguably the most diagnostic element for resolving species within the clade. The holotype parietal of *Nasutuceratops* (UMNH VP 16800) is nearly complete, preserving the entire median bar and most of the transverse bar, together with most of the lateral parietal ramus on the right side (Fig. 35). It appears to pertain to a sub-adult individual, being relatively thin and fragile, with the surface texture consisting of a mosaic of striated subadult and mottled adult texture (Sampson et al., 1997). However, the epiparietal ossifications are present and almost completely fused onto the marginal

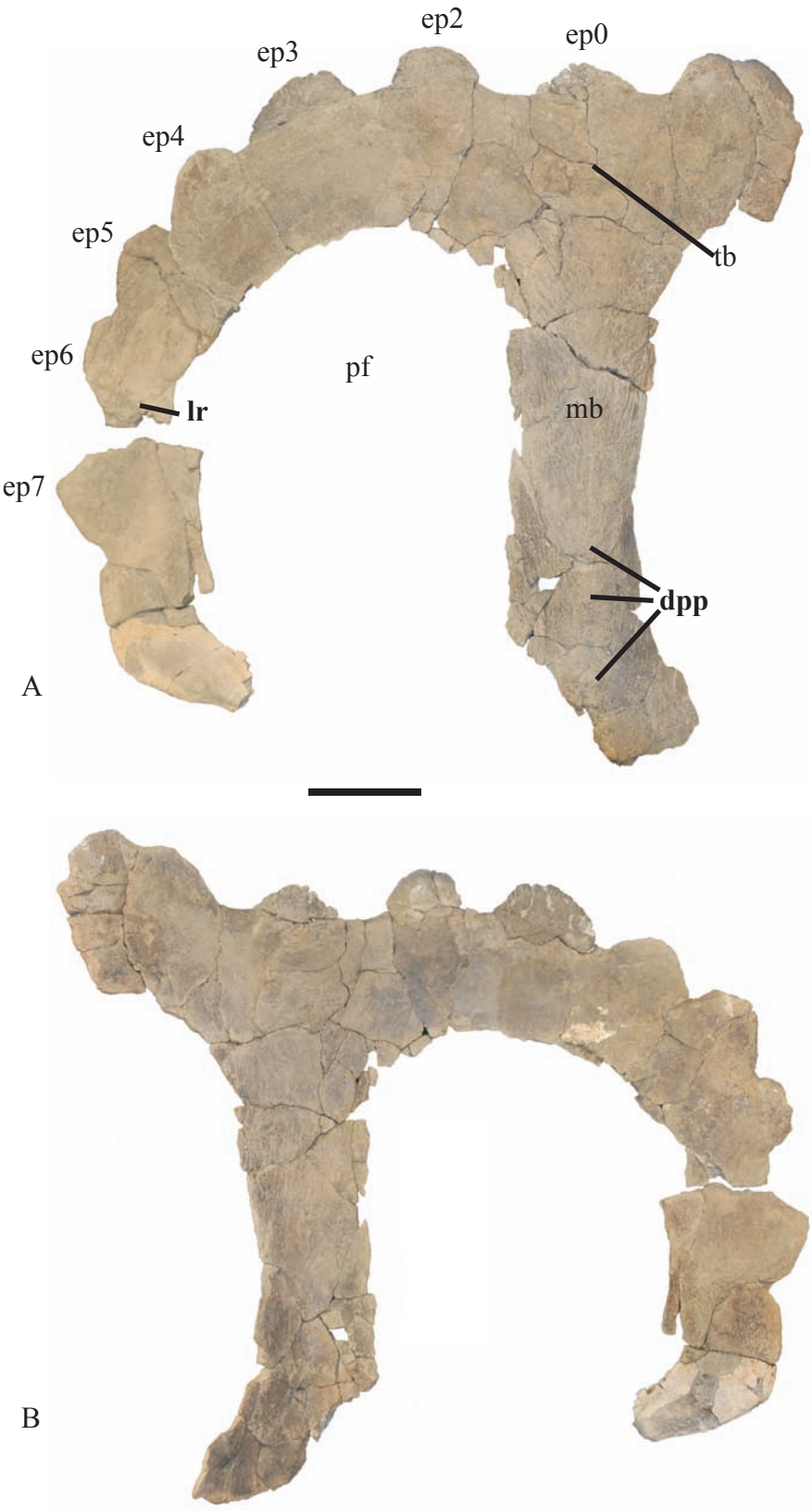

Figure 35. Photographs of the holotype parietal UMNH VP 16800. **A**, dorsal view; **B**, ventral view. **Abbreviations**: **dpp**, dorsal parietal process; **ep**; epiparietal; **lr**, lateral ramus; **mb**; midline bar; **pf**, parietal fenestra; **tb**, transverse bar. Scale bar = 10 cm.

undulations, a feature typically associated with adults. The latter feature, combined with others (e.g., extremely large supraorbital horncores) suggests that this animal was approaching adult status at the time of death.

The parietal includes six marginal undulations per side, as well as a median undulation, each topped by an epiparietal. A caudomedian epiparietal is otherwise present only in the chasmosaurine *Triceratops* (Marsh, 1889), and the centrosaurine *Avaceratops* (Dodson, 1986). Also in contrast to the standard centrosaurine condition, the frill is rounded caudomedially, with no indication of a median embayment. Imbrication of the marginal epiparietals on the lateral margin, a wavy appearance seen in most centrosaurines (Sampson et al., 1997; Ryan et al., 2001), also appears to be absent in this specimen. The symmetry or asymmetry of the parietal cannot be assessed due to erosional loss of most of the left transverse and lateral parietal rami.

The median bar is dorsoventrally thin (~4 mm in UMNH VP 16800) near the margins, thickening towards the midline (~15 mm), with an overall strap-like conformation similar in morphology to the midline parietal bar in *Achelousaurus* (e.g., MOR 485). Rostrally, the median bar is dorsally convex, forming a low, rounded median ridge bearing five midline undulations of varying height; the latter feature is highly variable within centrosaurines. The bar widens caudally near the apex of the parietal fenestrae to transition into the transverse parietal bar, which is similarly broad and strap-like. As is typical of other centrosaurines, the midline parietal bar splits rostrally into a pair of projecting prongs that form the caudal margin of the frontal fontanelle.

The rostrally-directed right lateral parietal ramus rounds out the frill and encloses the parietal fenestrae. The lateral ramus is thickest near the lateral edges where it is

associated with the marginal undulations and epiparietals, and thinnest medially toward the apature of the fenestrae. The holotype parietal (UMNH VP 16800) is approximately 19 mm thick along the lateral margins between the epiparietals, thinning to approximately 4 mm medially along the fenestral border.

Overall, the parietal of *Nasutuceratops* differs considerably from that of other centrosaurines, being subrectangular along the transverse and lateral parietal rami, lacking a caudomedian embayment, possessing a caudomedian epiparietal, and lacking any indication of the well developed hooks or spikes typical of other centrosaurines (e.g., *Centrosaurus*, *Styracosaurus*, *Pachyrhinosaurus*), including basal forms (e.g., *Diabloceratops, Albertaceratops*). Although it is conceivable that these processes would have developed into larger structures had this animal reached full maturity, this alternative is considered improbable, given the presence of fused epiparietals on the frill margins together with other indicators of advanced maturity (e.g., extremely large supraorbital horncores).

The epiparietals are low, roughly crescentic, asymmetrical and wedge shaped, with a slightly concave ventral surface. For the most part, these ossifications project outward in the same plane as the underlying parietal, although with a slight ventral flexion (Fig. 36). For the most part, the epiparietals are subequal in size, but become slightly smaller rostrally, as is typical. The external surfaces of the epiparietals are highly vascularized and rugose, and most likely supported a keratinous sheath in life.

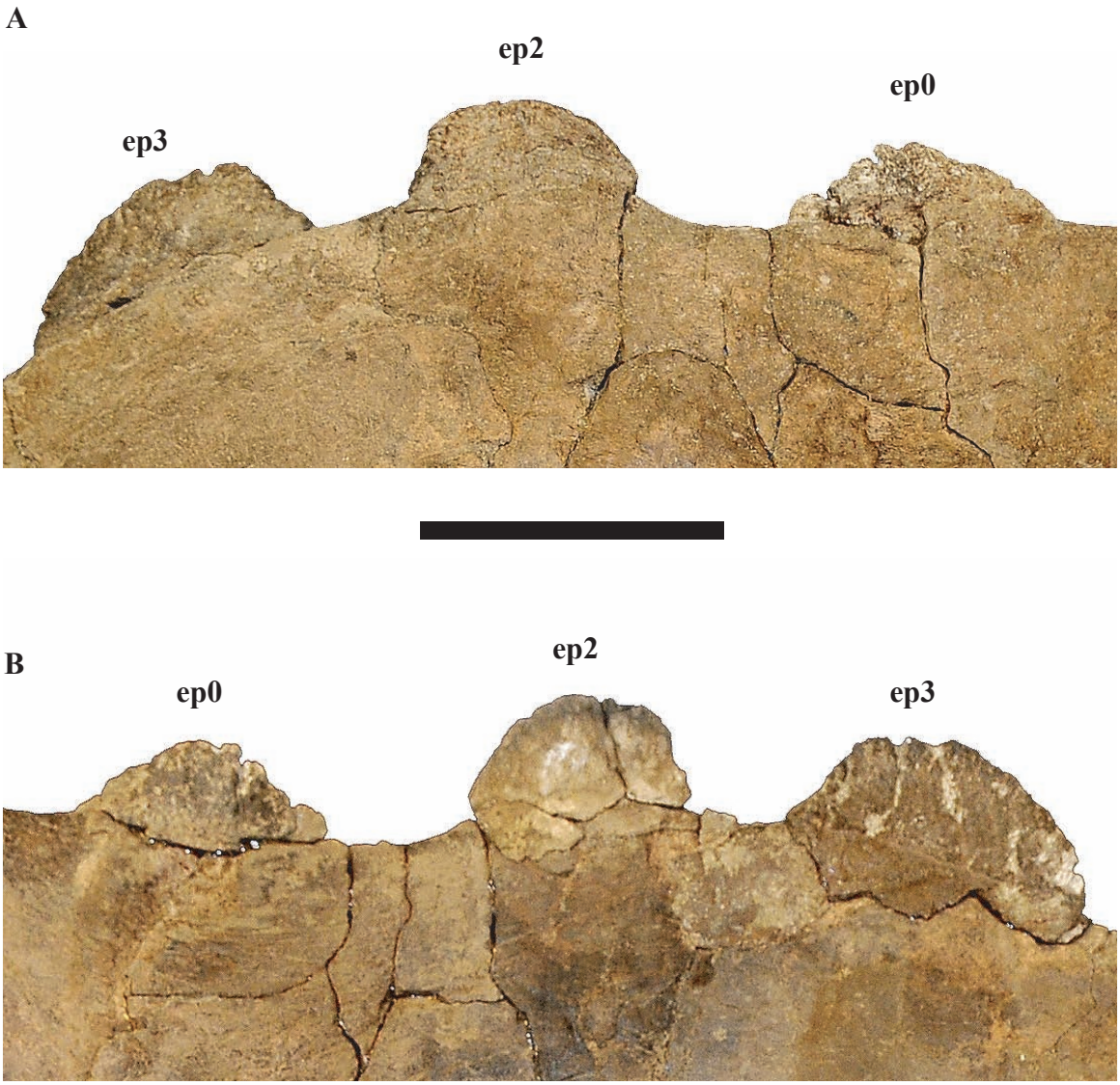

Figure 36. Photographs of the holotype epiparietals UMNH VP 16800. **A**, dorsal view; **B**, ventral view. **Abbreviations**: **ep**, epiparietal. Scale bar = 10 cm.

Mandible

Coronoid Process

The sole element of the mandible known for *Nasutuceratops* is the coronoid process, and only the rostral portion of the left coronoid process is preserved with the holotype specimen (UMNH VP 16800). Overall the element is typical of ceratopsids, although it does possess a highly rugose and pinched dorsal margin (Fig. 37).

Postcranial Skeleton

Axial Skeleton

Together with a nearly complete syncervical, multiple fragments of two dorsal vertebrae and one nearly complete dorsal vertebra are preserved with the holotype specimen. As is typical of all ceratopsids, the atlas and axis plus cervicals 3 and 4 completely coalesce in *Nasutuceratops* to form the syncervical (Parks, 1921; Lull, 1933; Brown and Schlaikjer, 1940a; Sternberg, 1951; Langston, 1975; Sereno, 1986; Dodson et al., 2004). The syncervical of *Nasutuceratops* is nearly complete, missing only portions of the neural spines and fragments of the coalesced centra (Fig. 38). The cranial end of the first cervical preserves the characteristic deep socket for articulation with the occipital condyle. Although the syncervical in *Nasutuceratops* is fragmentary and crushed transversely, the element exhibits typical ceratopsid morphology, being most similar to that of other centrosaurines (e.g., *Centrosaurus*, *Styracosaurus*).

The dorsal vertebrae are also typical of ceratopsids, with the centra being craniocaudally abbreviated and the neural arches being relatively tall neural (Fig. 39; Dodson et al., 2004). The articular faces of the preserved centra are subcircular to pear

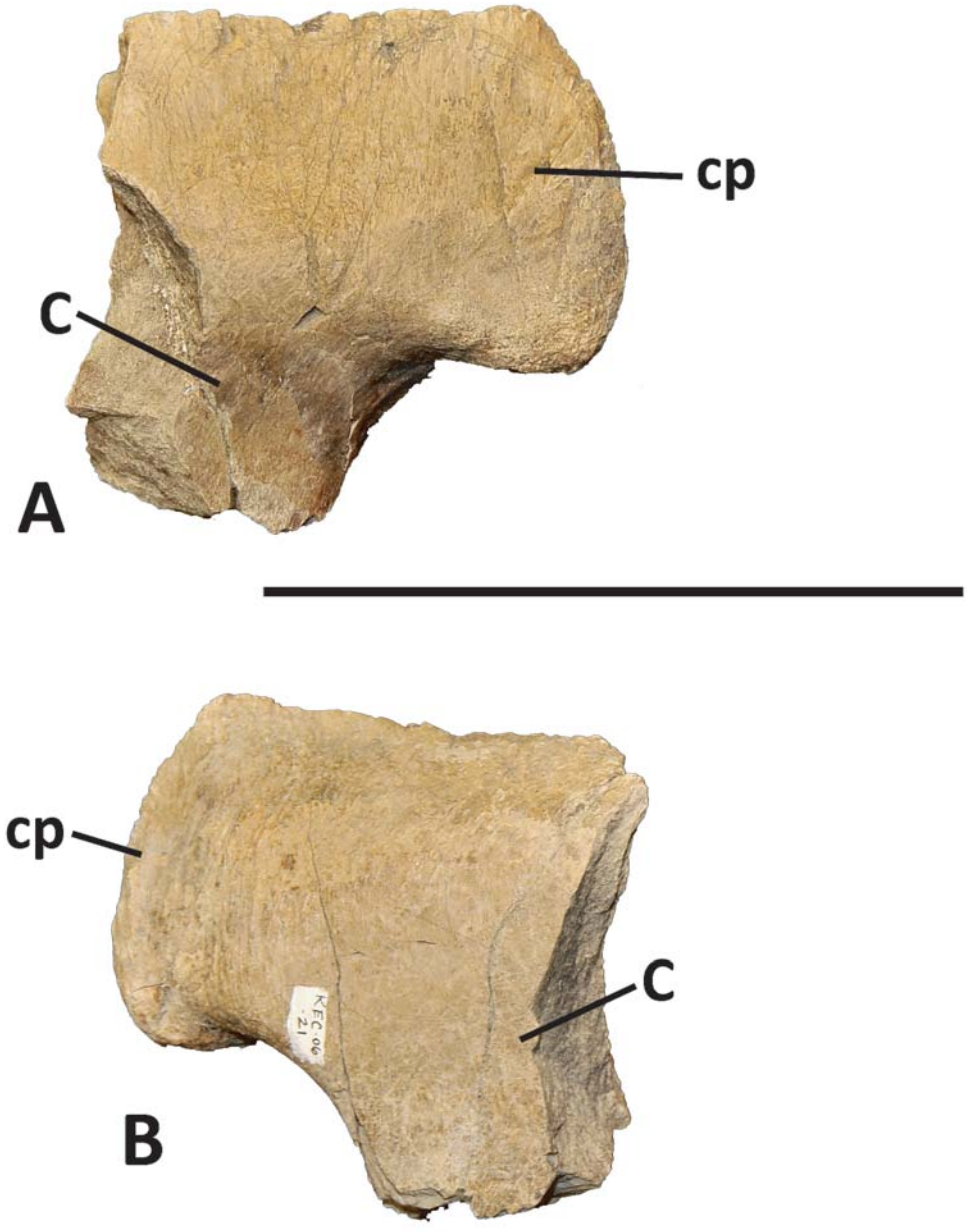

Figure 37. Photographs of the holotype coronoid process UMNH VP 16800. **A**, lateral view; **B**, medial view. **Abbreviations**: **c**, coronoid; **cp**, coronoid process. Scale bar = 10 cm.

Figure 38. Photograph of the holotype syncervical in right lateral view UMNH VP 16800. **Abbreviations**: **ivf**, intervertebral foramen; **stv**, sutural trace between vertebrae. Scale bar = 10 cm.

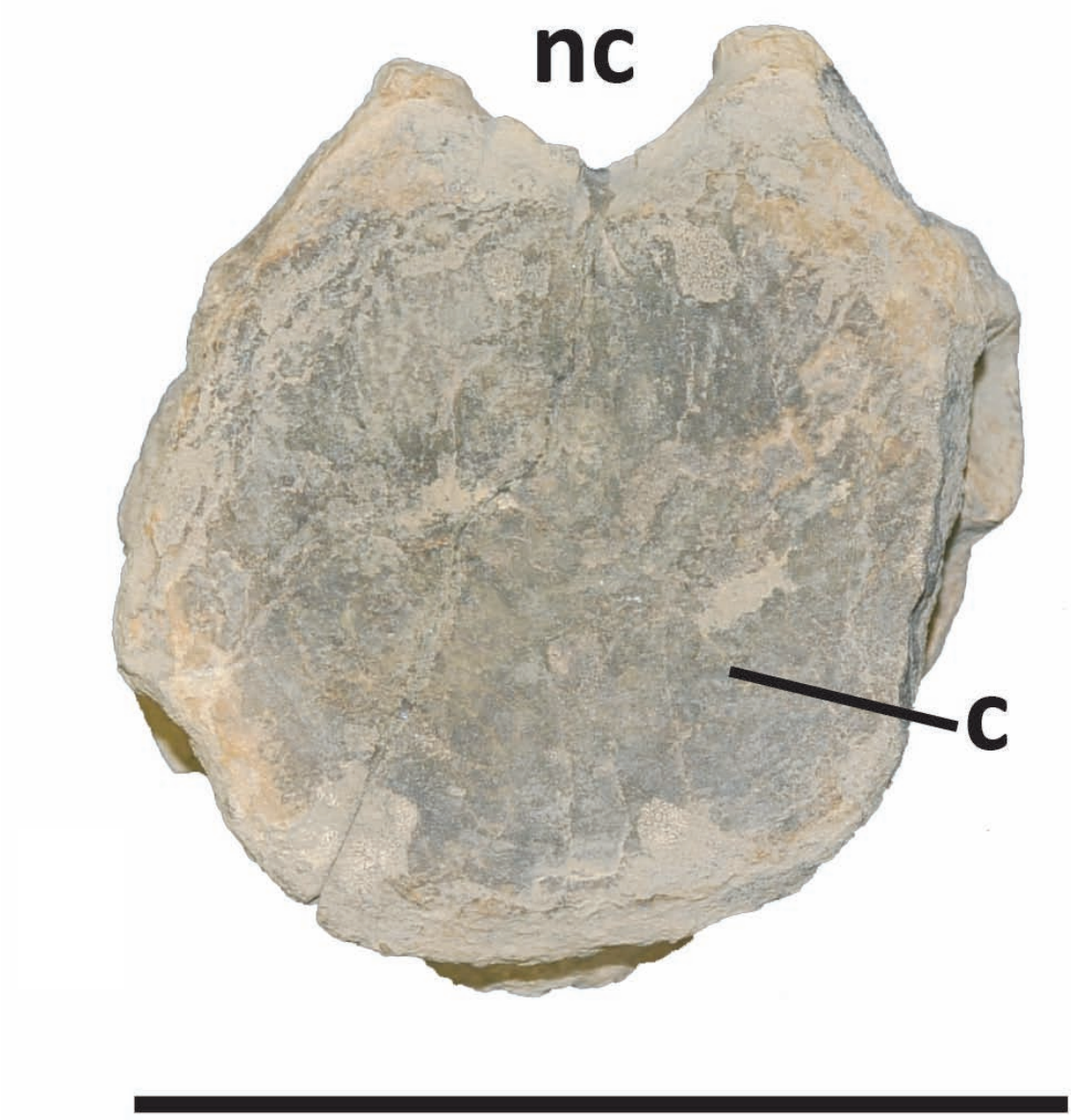

Figure 39 Photograph of a dorsal centrum from the holotype UMNH VP 16800. **Abbreviations**: **c**, centrum; **nc**, nueral canal. Scale bar = 10 cm.

shaped, most closely resembling those present on dorsal vertebrae of *Styracosaurus*, but they are generally similar to the morphology of centrosaurine dorsal vertebrae. The transverse processes associated with the nearly complete dorsal vertebra are strongly elevated, and the zygapophyses are prominent, as is typical for ceratopsids.

Appendicular Skeleton

A nearly complete left forelimb—including coracoid, scapula, humerus, and radius and ulna—is preserved with the holotype (Figs. 40-44). Additionally, this specimen includes portions of the right forelimb—including the caudodorsal blade of the scapula, proximal end of the humerus, fragments of the radius, and a nearly complete ulna. The left scapula, coracoids, humerus, ulna and radius were all recovered in articulation. Several patches of integument impressions were preserved in association with the left humerus and scapula (see below).

Scapula

The left scapula of UMNH VP 16800 is nearly complete, missing only a portion of the caudodorsal blade (Fig. 40). Conversely, only the caudodorsal blade of the right scapula is preserved. The scapula resembles that of other centrosaurines (Dodson et al., 2004), being long and relatively slender, with a flared and flattened caudal end and a scapular spine that extends from the caudal margin of the supraglenoid ridge along the caudodorsal blade. The scapula forms approximately two-thirds of the caudal portion of the glenoid fossa. Holding the scapula with the glenoid fossa in the horizontal plane, the caudodorsal blade is flattened transversely along the caudal end as well as being

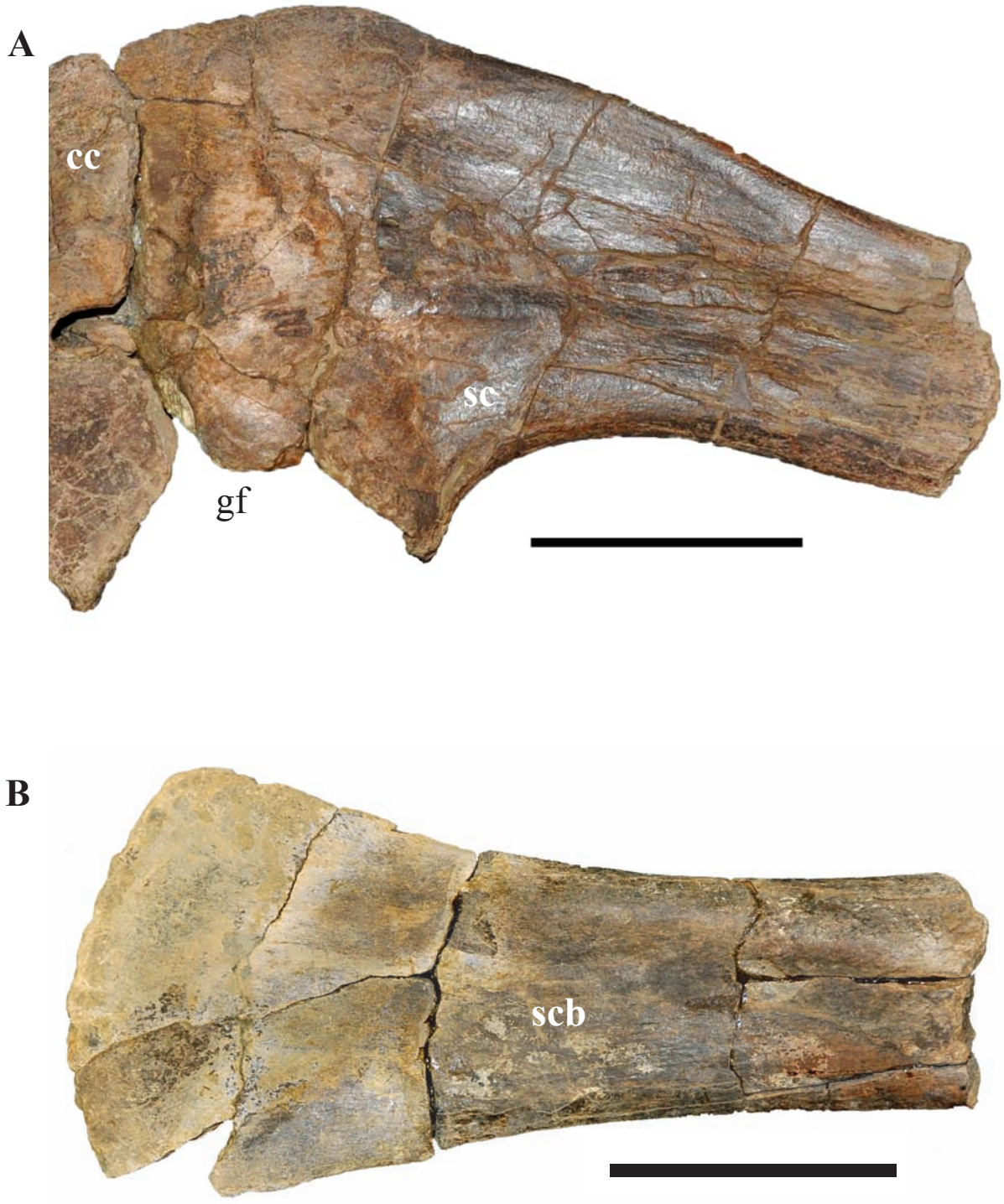

Figure 40. Photographs of the holotype scapula UMNH VP 16800. **A**, left side lateral view; **B**, right side lateral view. **Abbreviations**: **cc**, coracoid; **gf**, glenoid fossa; **sc**, scapula; **scb**, scapular blade. Scale bars = 10 cm.

dorsoventrally expanded. The caudal margin of the caudal end of the caudodorsal blade bears prominent muscle attachment scars. The thickest portion of the scapula is located immediately dorsal to the glenoid fossa. Overall, the scapula of the *Nasutuceratops* holotype (UMNH VP 16800) closely resembles that described for other centrosaurines (e.g., *Centrosaurus*, AMNH 5351).

Coracoid

As often occurs in ceratopsids, the left coracoid of UMNH VP 16800 is fused onto the proximal end of the scapula, and this element forms approximately one-third of the glenoid fossa (Dodson et al., 2004). The nearly complete coracoid is roughly square, lacking the prominent caudal process typical of other ceratopsids; however, this conformation is most likely the result of breakage (Fig. 41). The coracoid is ventrally flexed, giving the element a slight concavity on the ventral surface. As is typical of all ceratopsid coracoids, a large neurovascular foramen is present on the caudomedial portion of the coracoid immediately cranial to the scapular contact. Overall, the coracoid of *Nasutuceratops* is closely similar in morphology to that of other centrosaurines (e.g., *Centrosaurus*, AMNH 5351).

Humerus

The complete left humerus in the holotype (UMNH VP 16800) exhibits typical ceratopsid morphology, possessing a hemispheric and eccentric humeral head and a prominent deltopectoral crest that extends distally more than half the length of

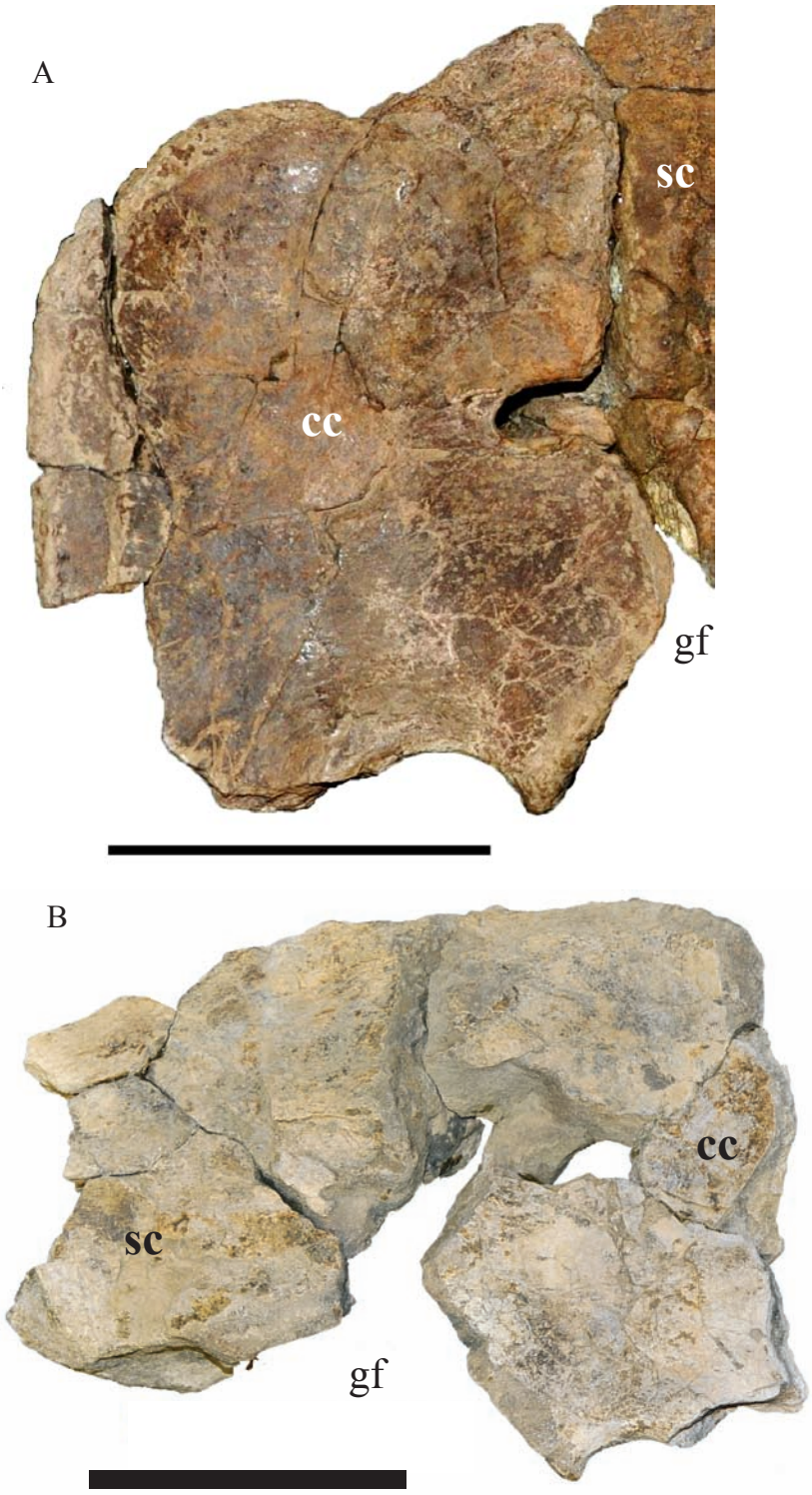

Figure 41. Photographs of the holotype coracoid UMNH VP 16800. **A**, left side lateral view; **B**, right side lateral view. **Abbreviations**: **cc**, coracoid; **gf**, glenoid fossa; **sc**, scapula. Scale bars = 10 cm.

the humerus (Fig. 42). The deltopectoral crest possesses a curved lateral margin, closely resembling the condition in *Centrosaurus* (e.g., TMP 2002.068.0083; Lehman, 1989; Lucas et al., 2006). As is more typical of centrosaurines than chasmosaurines, the distal end is less rugose in texture and only modestly expanded (Dodson et al., 2004). The right humerus in the holotype is fragmentary, lacking most of the distal end. Overall the humerus is relatively long and slender, but is otherwise typical of ceratopsids.

Ulna

An articulated left ulna and disarticulated right ulna were recovered with the holotype (UMNH VP 16800; Fig. 43). As is typical of ceratopsids, the ulna possesses a pronounced olecranon process for articulation with the distal end of the humerus. However, in contrast to a previous discussion of centrosaurine ulnae (Adams, 1988), the olecranon process in UMNH VP 16800 rivals that of chasmosaurines, more closely resembling the condition in *Agujaceratops mariscalensis* (UTEP P.37.7.086) than in *Centrosaurus apertus* (Lehman, 1989; Lucas et al., 2006). The most robust portion of the ulna occurs proximally, whereas the distal end is transversely narrow.

Radius

Together with a complete left radius, fragments of the right radius are preserved in the holotype specimen (UMNH VP 16800). The radius is thin overall, with expanded ends typical of other ceratopsids. The expanded proximal end is semicircular in expression, whereas the distal end is expanded and transversely narrow (Fig. 44).

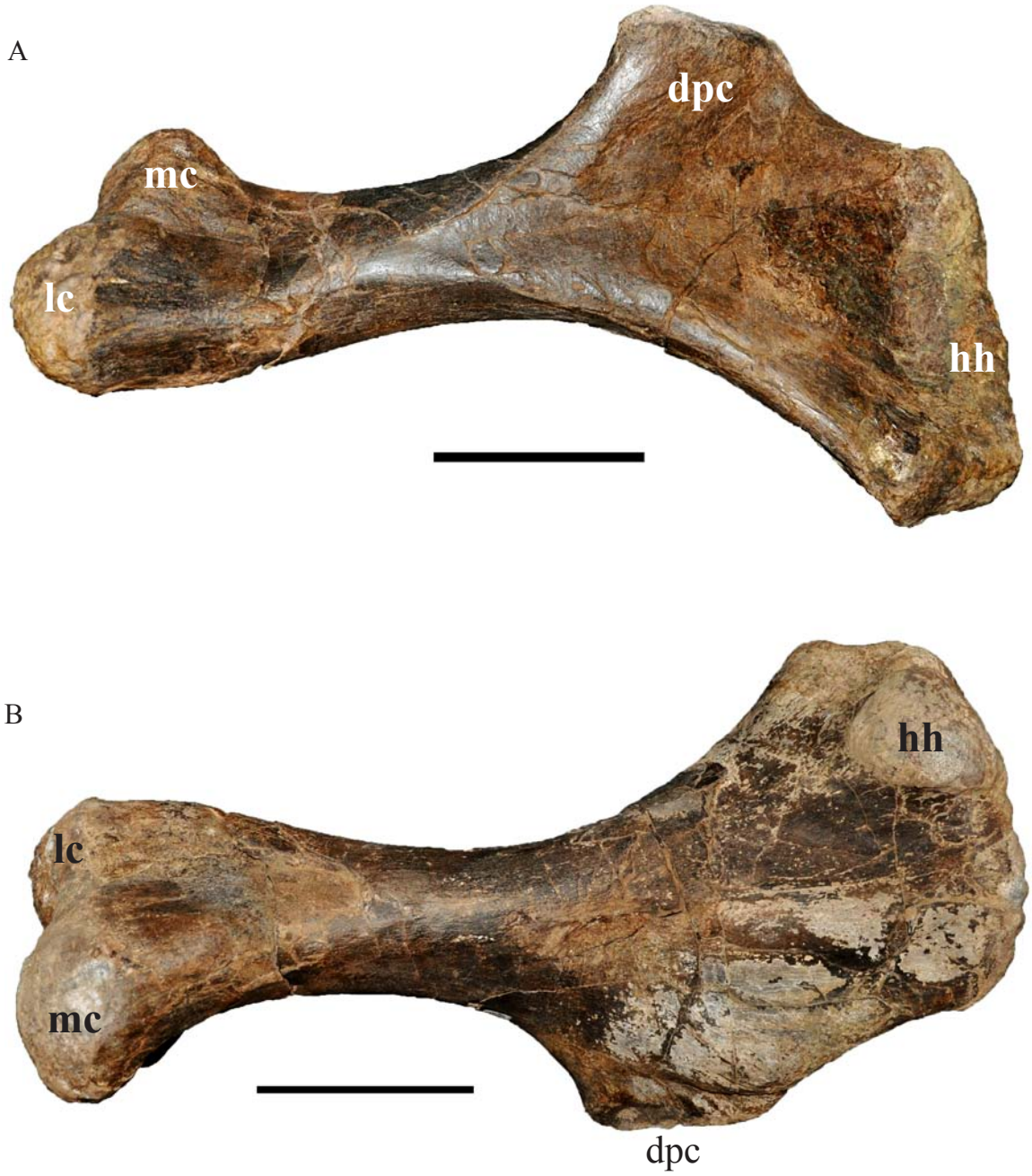

Figure 42. Photographs of the holotype humerus UMNH VP 16800. **A**, left humerus, lateral view; **B**, left humerus medial view. **Abbreviations**: **dpc**, deltopectoral crest; **hh**, humeral head; **lc**, lateral condyle; **mc**, medial condyle. Scale bars = 10 cm

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Figure 43. Photograph of the holotype ulna UMNH VP 16800. **Abbreviations**: **op**, olecranon process; **us**, ulnar shaft. Scale bar = 10 cm.

Figure 44. Photograph of the holotype radius UMNH VP 16800. Scale bar = 10 cm.

Integument

Skin Impressions

Several patches of integument impressions are preserved in association with the scapula and humerus of UMNH VP 16800 (Figs. 45-47). This is the only occurrence of ceratopsid integumentary impressions from GSENM, and one of only a handful known (Lambe, 191; Brown, 1917; Sternberg, 1925; Lull, 1933; Mayr et al., 2002). The skin impressions in UMNH VP 16800 occur as both casts and molds, showing three different tubercle patterns. The tubercles differ from those described for ornithopod (e.g., hadrosaur) integument impressions, which are relatively common finds (Osborn, 1911; Brown, 1916; Lull and Wright, 1942; Horner, 1984; Hall et al., 1988; Anderson et al., 1996; Anderson et al., 1998; Anderson et al., 1999; Gillette, 2002; Murphy et al., 2002; Wegweiser et al., 2004; Lund, 2006; Lund, 2008). Integument patch "A" is an array of tightly packed pavement tubercles associated with the left humerus just below the humeral head along the caudal margin of this element. The tubercles range in diameter from 2mm to 8mm, increasing in size away from the humerus; they are subcircular to elliptical in shape, and preserved in positive relief (Fig. 45). Integument patch "B" is an array of larger, loosely packed pavement tubercles associated with the left humeral head, adjacent to the glenoid fossa, that range in diameter from 5 mm to 11 mm. The pavement tubercles in patch "B" are preserved in greater relief as both cast and mold, and are much more elliptical in shape than those in patch "A" (Fig. 46). The most notable integument impression, patch "C", associated with *Nasutuceratops*, is preserved as both cast and mold, and is expressed as raised hexagonal tubercles framed by prominent triangular grooves (Fig. 47). Integument patch "C" is associated with the left humeral head between

Figure 45. Photograph of integument impression patch “A” associated with the holotype left forelimb. Scale bar = 10 cm.

Figure 46. Photograph of integument impression patch “B” associated with the holotype left forelimb. Scale bar = 10 cm.

Figure 47. Photograph of integument impression patch “C” associated with the holotype left forelimb. Scale bar = 10 cm.

patches “A” and “B”. The hexagonal tubercles of patch “C” range in size from 8 mm to 11mm.

PHYLOGENETIC ANALYSIS

Methods

Ceratopsidae has been the focus of several cladistic analyses (Sereno, 1986; Pisani et al., 2002; Dodson et al., 2004), with the most recent being that of Ryan (2007). The majority of these analyses have been limited in breadth to a particular subset or portion of the clade (e.g., basal ceratopsians—Chinnery and Weishampel, 1998; Sereno, 2000; Xu et al., 2002; Centrosaurinae—Sampson, 1995; Penkalski and Dodson, 1999; Currie et al., 2008; Chasmosaurinae—Forster et al., 1993; Forster, 1996b; Lehman, 1996; Holmes et al., 2001). The present analysis is a subset of a larger analysis encompassing Ceratopsidae (Sampson et al., unpublished data).

Centrosaurinae has long been established as a monophyletic taxon (Lambe, 1915; Sternberg, 1949; Lehman, 1990; Dodson and Currie, 1990; Sampson, 1995; Penkalski and Dodson, 1999; Dodson et al., 2004; Ryan and Russell, 2005; Ryan, 2007; Currie et al., 2008). In order to resolve the historical relationships of *Nasutuceratops titusi*, a species-level cladistic analysis was conducted of Centrosaurinae consisting of 155 characters arrayed across 12 ceratopsid in-group taxa and 11 out-group taxa; *Leptoceratops gracilis*, *Bagaceratops rozhdestvenskyi*, *Magnirostris dodsoni*, *Turanoceratops tardabilis*, *Protoceratops andrewsi*, and *Zuniceratops christopheri* represent successively more basal ceratopsian out-groups; and *Chasmosaurus belli*,

Chasmosaurus russelli, *Chasmosaurus kaiseni*, *Pentaceratops sternbergi*, and *Triceratops horridus* represent Chasmosaurinae. All currently recognized centrosaurine species were included (*Centrosaurus apertus* Lambe, 1904, *Styracosaurus albertensis* Lambe, 1913, *Pachyrhinosaurus canadensis* Sternberg, 1950, *Avaceratops lammersi* Dodson, 1986, *Achelousaurus horneri* Sampson, 1995, *Einiosaurus procurvicornis* Sampson, 1995, *Centrosaurus brinkmani* Ryan and Russell, 2005, *Albertaceratops nesmoi* Ryan ,2007, *Pachyrhinosaurus lakustai* Currie et al., 2008, *Diabloceratops eatoni* Kirkland and DeBlieux, in press, *Rubeosaurus* [*Styracosaurus*] *ovatus* McDonald and Horner, in press). The data matrix (Table 3) is adapted primarily from Sampson (1995), Dodson et al. (2004), Ryan (2007), Currie et al. (2008), and Sampson et al.,(unpublished data), although modified to incorporate new information resulting from this study. The data matrix was created using Mesquite 2.71 (Maddison and Maddison, 2009). A limited number of postcranial characters were utilized in this analysis for the following reasons: 1) within-group phylogenetic relationships of ceratopsids have previously been diagnosed primarily on craniofacial characters; 2) postcranial materials for some taxa are poorly known; and 3) postcranial characters have been shown to be of limited usefulness in higher level analyses of ceratopsids (Chinnery, 2004). Appendix A includes a complete, annotated list of characters and character states modified after Sampson (1995), Ryan (2007), Currie et al., (2008), and Sampson et al., (unpublished data). Character determination for each taxon was obtained from firsthand specimen observations and, where necessary, augmented with the current literature. The phylogenetic analysis was run using Tree Analysis Using New Technology (TNT) 1.1 (Goloboff et al., 2008), and optimized using DELTRAN optimization.

A total of 18 characters in this analysis (52, 61, 69, 70, 76, 77, 79, 87, 89, 95, 98, 99, 102, 107, 109, 110, 111, 112) are multistate (i.e., possessing more than one character state). Conventionally, multistate characters are excluded from analysis due to the difficulty in trying to order and polarize such characters (Forey et al., 1998). However, due to variation among ceratopsids being restricted, for the most part, to the dorsal skull roof and cranial ornamentation, the separation of these apomorphies is problematic (Ryan, 2007). In particular, problems arise when attempting to subdivide multistate characters into distinct valid entities in such a manner that each is wholly independent of the others; a problematic consequence of such subdivision is the addition of large amounts of missing data to the data set. In order to understand the support for the generated clades, the analysis was subjected to a standard bootstrap analysis consisting of 1000 iterations using all characters that were subjected to 50% resampling. Additionally, a Bremer decay analysis was performed to determine the number of additional steps required to collapse each node. Two characters—character 38, nasal ornamentation type in adult; and character 78, frontal fontanelle—were run ordered in this analysis due to detailed information from ontogenetic series in specimens.

The consistency index was calculated by the following formula: $CI = \frac{M}{S}$; where M is the total number of character changes expected, given the data set, and where S is the actual number of changes that occur in the tree (McCarthy, 2009). Of the 155 total characters in the analysis, 137 are two-state characters, 10 are three-state characters, 6 are four-state characters, and 2 are five-state characters, for a total of 178 expected changes (i.e., M= 178). The value for S is taken from the tree length, the actual number of changes that occurred in the tree (i.e., S= 264). The retention index was calculated by the

following formula: $RI = [\frac{G-S}{G-M}]$, where M and S are the same variables used to calculate CI, and where G is the greatest number of steps characters can have in any cladogram (McCarthy, 2009). For the 23 taxa of this phylogenetic analysis the maximum number of steps characters can have is 1099 (i.e., G = 1099).

Results

The analysis produced two most parsimonious trees. The strict consensus tree has a length of 264 steps, a consistency index (CI) of .674, and a retention index (RI) of .907 (Fig. 48). Monophyly of Ceratopsidae is supported by two unambiguous characters (32, 143). Centrosaurinae is supported by eight characters (1, 5, 6, 18, 41, 69, 90, and 95), and Chasmosaurinae is supported by 13 characters (7, 11, 14, 19, 30, 31, 35, 37, 60, 76, 81, 82, and 94; Fig. 48). Bremer support for the clade Ceratopsidae is three steps; for Centrosaurinae it is two steps; and for Chasmosaurinae it is six steps. The basal neoceratopsians *Turanoceratops* and *Zuniceratops* form an unresolved dichotomy and are placed as the sister group to Ceratopsidae. *Nasutuceratops* is unequivocally placed within Centrosaurinae, requiring eight steps to remove it from this clade, and a subsequent 13 steps to place it within Chasmosaurinae (Fig. 48). The new Utah taxon falls out as the sister taxon to *Avaceratops* from the late Campanian of Montana, with the clade supported by three unambiguous synapomorphies (112, 114, 126). The sister group to *Nasutuceratops* + *Avaceratops* [(*Albertaceratops* + (*Einiosaurus* + (*Achelousaurus* + (*Pachyrhinosaurus*)))] is supported by three unambiguous characters (31, 60, 67).

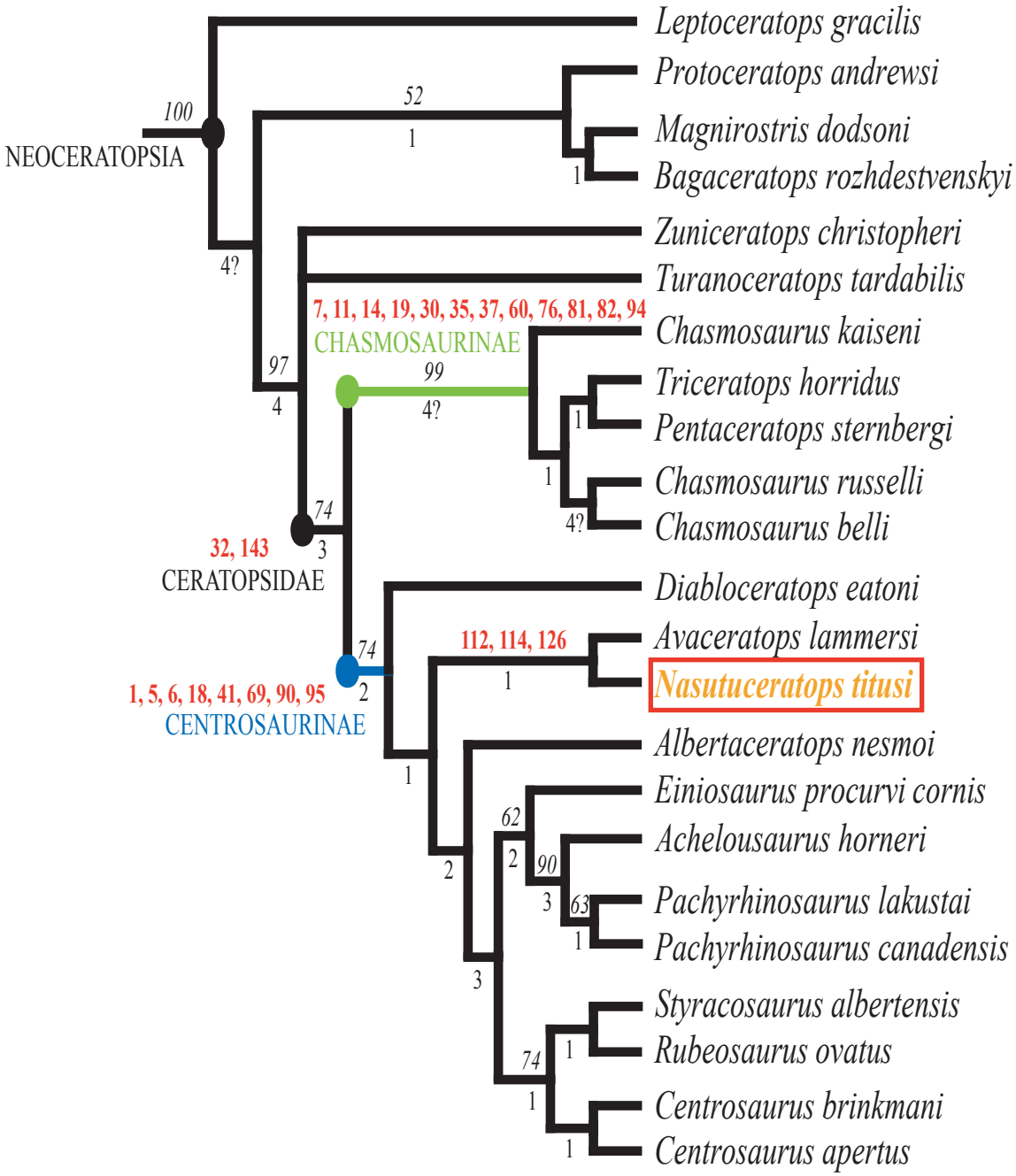

Figure 48. Strict consensus of the two most parsimonious trees obtained from the phylogenetic analysis. Percent support for clades from unordered bootstrap analysis (1,000 replicates) are listed above the branches in italicized numbers. Bremer support for clades are listed below the branches. Characters diagnosing nodes listed above the stems in red. Additional tree statistics: characters = 155; steps = 264.

DISCUSSION

Taxonomic and Phylogenetic Implications

The ceratopsid fossil record is arguably the best sampled for any major group of dinosaurs, with approximately 30 recognized species known from a narrow stratigraphic and geographic ranges (Dodson et al., 2004; Sampson and Loewen, in press; Table 4). Understanding variation is a key element in any rigorous phylogenetic analysis. The exceptional fossil record of ceratopsids—including numerous monospecific bonebeds—provides researchers the unique opportunity to gain insights into both inter- and intrasecific variation, including ontogeny (Lehman, 1989; Rogers, 1990; Ryan, 1992 Sampson, 1995; Sampson et al., 1997; Sampson and Ryan, 1997; Currie et al., 2008). The holotype of *Nasutuceratops* (UMNH VP 16800) can be confidently placed within Centrosaurinae on the basis on several synapomorphies, including crescentic rostral; semicircular, hypertrophied premaxilla with expanded ventral margin, and dorsal ascending ramus that slots into the nasals; narial spine formed from premaxilla and nasal; stepped squamosal (present in all centrosaurines except *Avaceratops*); and, as compared to chasmosaurines, a relatively abbreviated parietosquamosal frill. The inferred morphologies for incomplete or missing elements (e.g., jugal, and squamosal; see below) also support this assessment. The recovery of *Nasutuceratops* as a relatively basal taxon within Centrosaurinae is supported by several plesiomorphic characters. These include a ventrally displaced tooth row and elongate and robust supraorbital horns. Within

Table 4 List of currently recognized ceratopsid taxa.

Taxon	Specimen Number	Formation	Location	Age
Diabloceratops eatoni	UMNH VP 16699	Wahweap	Southern Utah	late Camp.
Albertaceratops nesmoi	TMP 2001.26.01	Oldman	Alberta	late Camp.
Nasutuceratops titusi	UMNH VP 16800	Kaiparowits	Southern Utah	late Camp.
Avaceratops lammersi	ANSP 15800	Judith River	Montana	late Camp.
MOR Avaceratops	MOR 692	Judith River	Montana	late Camp.
Centrosaurus apertus	NMC 971	Dinosaur Park	Alberta	late Camp.
Centrosaurus brinkmani	TMP 2002.68.1	Oldman	Alberta	late Camp.
Rubeosaurus ovatus	USNM 11869/ MOR 492	Two Medicin	Montana	late Camp.
Styracosaurus albertensis	CMN 344	Dinosaur Park	Alberta	late Camp.
Einiosaurus procurvicornis	MOR 456-8-9-6-1	Two Medicin	Montana	late Camp.
Achelousaurus horneri	MOR 485	Upper Two Medicine	Montana	late Camp.
		Horseshoe Canyon,	Alberta	Maast.
Pachyrhinosaurus canadensis	NMC 8867	St. Mary River	Alberta	Maast.
		Prince Creek	Alaska	Maast.
Pachyrhinosaurus lakustai	TMP 1986.55.258	Wapiti	Alberta	Camp.-Maast.
Chasmosaurus belli	NMC 0491	Dinosaur Park	Alberta	late Camp.
Chasmosaurus russelli	CMN 8800	Dinosaur Park	Alberta	late Camp.
Chasmosaurus kaiseni	AMNH 5401	Dinosaur Park	Alberta	late Camp.
Chasmosaurus irvinensis	CMN 41357	Dinosaur Park	Alberta	late Camp.
New Kaiparowits Taxon B	UMNH VP 17000	Kaiparowits	Southern Utah	late Camp.
Agujaceratops mariscalensis	UTEP P.37.7.086	Aguja	Texas	Camp.
New Kaiparowits Taxon A	UMHH VP 16784	Kaiparowits	Southern Utah	late Camp.
Pentaceratops sternbergii	AMNH 6325	Fruitland, Lower Kirtland	New Mexico	Camp.-Maast.
Coahuilaceratops magnaquerna	CPC 276	Cerro del Pueblo	Mexico	Camp.
Anchiceratops ornatus	AMNH 5251	Horseshoe Canyon,	Alberta	Maast.
Arrhinoceratops brachyops	ROM 5135	Horseshoe Canyon,	Alberta	Maast.
		Lance	Wyoming	Maast.
		Kirtland	New Mexico	Maast.
Torosaurus latus	ANSP 15192	McRae	New Mexico	Maast.
		Javelina	Texas	Maast.
		Hell Creek	Montana	Maast.
		Frenchman	Saskatchewan	Maast.
Torosaurus utahensis	USNM 15583	North Horn	Utah	Maast.
Eotriceratops xerinsularis	RTMP 2002.57.7	upper Horseshoe Canyon	Alberta	Maast.
Nedoceratops hatcheri	USNM 2412	Lance	Wyoming	Maast.
		Lance	Wyoming	Maast.
		Hell Creek	Montana	Maast.
Triceratops horridus	YPM 1820	Hell Creek	North Dakota	Maast.
		Hell Creek	South Dakotas	Maast.
		Laramie	Colorado	Maast.
Triceratops prorsus	YPM 1822	Lance	Wyoming	Maast.
		Hell Creek	Montana	Maast.

Centrosaurinae, these features are otherwise present only in *Avaceratops*, *Albertaceratops* and *Diabloceratops*. Both features are also present in the basal neoceratopsian *Zuniceratops*, and elongate supraorbital horncores characterize all chasmosaurines except *Chasmosaurus*.

The basal position of the new Utah taxon is important for resolving key issues surrounding the evolution of short-frilled ceratopsids. For example, a number of features present in the skull of *Nasutuceratops* suggest that the polarization of several characters (e.g., orientation of dorsal ascending ramus of the premaxilla and maxilla, and rostrocaudal short maxilla) should be reversed, a finding that yields increased phylogenetic resolution of evolutionary patterns within the clade. Despite the suite of basal neoceratopsian (i.e., nonceratopsid) characters retained by *Nasutuceratops*, a number of other features suggest that this animal is derived relative to other centrosaurines. Whereas the bulk of centrosaurine species are diagnosed by two or three autapomorphies (Dodson et al., 2004; Ryan, 2007), *Nasutuceratops* is diagnosed by five unique, derived craniofacial characters: rostrocaudally abbreviated and dorsoventrally deep preorbital region comprising 75 % of preorbital skull length; extensively pneumatized nasals; greatly hypertrophied premaxilla-maxilla contact, maxilla possessing a double-faceted, medially directed flange contributing to a short hard palette; and extremely elongate and robust supraorbital ornamentation, the absolute longest within Centrosaurinae. In addition to the high number of autapomorphies, *Nasutuceratops* is unique among ceratopsids in that most of its autapomorphies do not appear to pertain to signaling and/or combat structures typically associated with mate competition and sexual selection (i.e., nasal and supraorbital horncores and parietosquamosal frill ornamentation;

Farlow and Dodson, 1975; Sampson et al., 1997; Dodson et al., 2004). Instead, most autapomorphies in this taxon occur in the facial skeleton and can be putatively associated with nonmating features modified under natural selection (see below). This finding, coupled with a much younger geologic age than other long-horned centrosaurines (e.g., *Avaceratops* (Dodson, 1986), *Albertacertops* (Ryan, 2007), and *Diabloceratops* (Kirkland and DeBlieux ,in press); Fig. 49), suggest that *Nasutuceratops* may be a member of a previously unknown radiation of short-faced, long-horned centrosaurines in the southern WIB, differing from the better known clade of northern centrosaurines not only in supraorbital and frill ornamentation, but also in the facial skeleton characters (i.e., short, deep preorbital facial skeleton).

The hypothesis that *Nasutuceratops* represents a previously unrecognized clade of southern centrosaurines depends on placement of *Diabloceratops* as the basalmost centrosaurine (Kirkland and DeBlieux, in press). First, *Diabloceratops* (Figs. 48, 49) possesses a facial skeleton more typical of other centrosaurines (e.g., *Albertaceratops*, *Centrosaurus*), indicating that the exceptionally deep (tall) snout of *Nasutuceratops* is derived rather than plesiomorphic. Second, the significantly greater geologic age (~ 79 Ma) of *Diabloceratops* is also consistent with its basal position, adding support to the hypothesis that it approximates the primitive condition for centrosaurines (Jinnah et al., 2009). Third, the geographic position of *Diabloceratops*, also found within GSENM in southern Utah, indicates that basal centrosaurines in the south were not somehow distinct from those in the north. In short, the unusual facial morphology present in skull of *Nasutuceratops* is best interpreted as derived in large part, because *Diabloceratops* represents our best understanding of basal Centrosaurinae morphology.

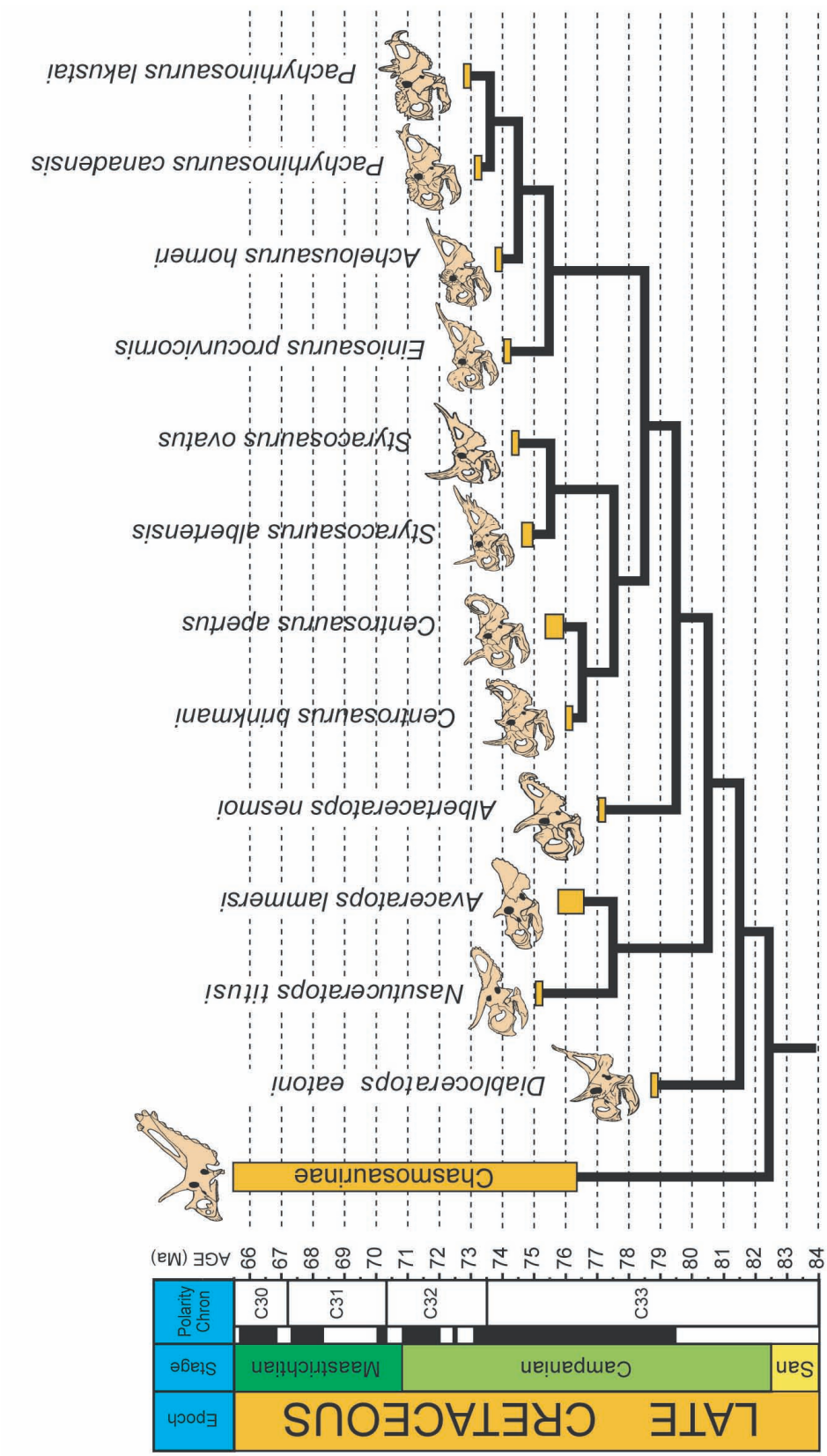

Figure 49. Temporally calibrated phylogeny of select centrosaurines including *Nasutuceratops titusi*, as well as Chasmosaurinae (After Clayton et al., 2009).

Functional Hypotheses

Nasutuceratops can be distinguished from all other centrosaurines by its extremely short, deep preorbital facial skeleton, morphologically distinct premaxilla and maxilla, highly pneumatic nasals, and extremely long and robust supraorbital ornamentation. The extremely short preorbital region is related both to the abbreviated maxilla and vertically inclined caudal ramus of the premaxilla. Functional adaptations associated with this morphology are unknown; however, possession of an abbreviated preorbital region may be related to morphological changes in basal ceratopsians toward more derived mastication functions. Such morphology would have increased the mechanical advantage during mastication by bringing the beak closer to the fulcrum (i.e., jaw joint) of the lower jaw (Ostrom, 1964, 1966). The deepness of the narial region is due in large part to the morphology of the premaxilla and maxilla, with both elements exhibiting steeply rising contact surfaces (Figs. 13, 15). The function of the enlarged contact surfaces between both the premaxilla and maxilla is unknown; however, given that these contacts are steeply inclined and more robust than those of more derived genera, this modification might feasibly be related to absorbing increased bite forces (Riu et al., 1960; Geist, 1971; Schaffer and Reed, 1972; Dyce et al., 1987).

As described above, pneumaticity within the nasal is likely derived from a paranasal air source invaginating rostrally. Among extant vertebrates, craniofacial pneumatics have previously been associated with a variety of functions, including moisture exchange (O'Malley, 1924; Eckert-Möbius, 1933; Witmer, 1997a), shock absorption (Riu et al., 1960; Geist, 1971; Schaffer and Reed, 1972; Dyce et al., 1987), vocalization resonance (Bignon, 1889; O'Malley, 1924; Eckert-Möbius, 1933; Wegner,

1958; Dyce et al., 1987), and bony weight reduction (Paulli, 1900; Negus, 1958; Möller, 1969; Schummer at al., 1979; Bühler, 1986; Winkler, 1979; Witmer, 1990; Witmer, 1995a; Witmer, 1995b; Witmer, 1997a; Witmer, 1997b; Witmer, 1999; Koppe et al., 1999; Witmer et al., 2004). At present, the function of the extensive nasal pneumaticity in *Nasutuceratops* remains unclear.

Long, robust supraorbital horncores were once thought to be diagnostic of Chasmosaurinae; however, the discoveries of *Zuniceratops*, *Avaceratops*, *Diabloceratops*, and *Albertaceratops*, now accompanied by *Nasutuceratops*, demonstrates that long supraorbital ornamentation are symplesiomorphic for the clade (Wolfe and Kirkland, 1998; Wolfe et al., 2007; Ryan, 2007; Kirkland and DeBlieux, in press). Many proposed functions have been postulated for the supraorbital ornamentation of ceratopsids, including intraspecific combat and display (Lull, 1933; Farlow and Dodson ,1975; Spassov, 1979; Sampson, 1997; Sampson et al., 1997), predator defense (Hatcher et al., 1907; Lull 1933), utilitarian uses such as knocking down vegetation (Tait and Brown, 1928), and thermoregulation (Barrick et al., 1998). Of these alternatives, mate competition, involving a combination of display and combat, has been the most widely accepted interpretation in recent years (e.g., Dodson et al., 2004).

If the latter hypothesis applies to the unique supraorbital horncores of *Nasutuceratops*, the rostrolateral orientation and torsional twist might have facilitated interlocking of horns with conspecific opponents, as in many extant bovid species (Lundrigan, 1996). Farke (2004) considered the supraorbital horncores of ceratopsids from a functional standpoint, using scale models to examine the probability that forms with elongate supraorbital horncores, such as *Triceratops,* locked horns during agonistic

interactions. Farke's results identified three plausible horn locking positions for *Triceratops* (i.e., single horn contact, full horn locking, and oblique horn locking) that may be relevant for *Nasutuceratops*. Additionally, Farke et al., (2009) examined cranial pathologies in adult specimens of both *Triceratops* and *Centrosaurus* that the authors postulated were related to conspecific combat in the two taxa. They concluded that periosteal bone lesions present in specimens of *Triceratops* are consistent with trauma inflicted during agonistic behavior. The results of Farke and colleagues were not as conclusive for specimens of *Centrosaurus*, but this finding in no way negates the hypothesis of an agonistic use for the supraorbital ornamentation in *Nasutuceratops*.

Stratigraphic, Biogeographic and Evolutionary Implications

Biogeographic studies of Mesozoic vertebrates have emphasized intercontinental faunal comparisons. However, research involving Upper Cretaceous formations deposited in the WIB of North America offer the potential for finer-scale, intracontinental biogeography. Extending across a temporal span of 25 million years, a Late Cretaceous epeiric sea divided continental North America into two separate east and west landmasses—Laramidia to the west and Appalachia to the east (Williams and Stelck, 1975; Lehman, 1997; Scotese, 2001, 2002) . Although fluctuating, the total habitat area available for terrestrial and freshwater vertebrates on Laramida is estimated to have been about 16% of the total area of present day North America (Lehman, 1997; Scotese, 2001). During the final two stages of the Late Cretaceous, the Campanian and Maastrichtian, numerous fossiliferous formations, terrestrial and marine, were deposited east of the Sevier orogenic belt (Lehman, 1997; Scotese, 2001, 2002). One such unit is

the Kaiparowits Formation, deposited in the south-central region of the WIB when North America occupied a paleolatitude of approximately 45º north (Lehman, 1997; Scotese, 2002; Fig. 50). Geologic studies by Roberts et al., (2005) and Roberts (2007) included identification and analysis of eight bentonitic clay (volcanic ash) layers intercalated throughout the 860 meter thick formation, yielding a late Campanian absolute age range for the Kaiparowits Formation in GSENM of ~76.1-74.0 Ma (Fig. 6). Combined with previously published radiometric dates for other fossiliferous formations of the WIB, this work shows the Kaiparowits Formation to be contemporaneous or penecontemporaneous with several of the most fossiliferous formations of North America (e.g., Dinosaur Park Formation, Alberta; upper Judith river and Two Medicine formations, Montana; Fruitland Formation and lower Kirtland Formation, New Mexico; upper Aguja Formation, Texas) (Goodwin and Deino, 1989; Rogers et al., 1993; Eberth and Hamblin, 1993; Fassett and Steiner, 1997; Fig. 51).

The northern portion of the WIB has been sampled extensively for ceratopsid dinosaurs. Of the 32 recognized ceratopsid species, 15 taxa (nearly one-half of the total known diversity) are from Alberta and Montana alone (Sampson and Loewen, in press). In contrast, the southern region of the WIB has remained relatively enigmatic with respect to ceratopsids and centrosaurines in particular. Recent finds from Utah, New Mexico and Coahuila (Mexico) are providing key insights into a previously unknown array of southern ceratopsids that may rival the horned dinosaur diversity in the north (Sweeney and Boyden, 2003; Sampson et al., 2004; Lucas et al., 2006; Lund et al., 2007; Sampson and Loewen, in press; Sampson et al., in press; Loewen et al., in press). Two newly discovered southern centrosaurines from GSENM, *Nasutuceratops titusi* from the

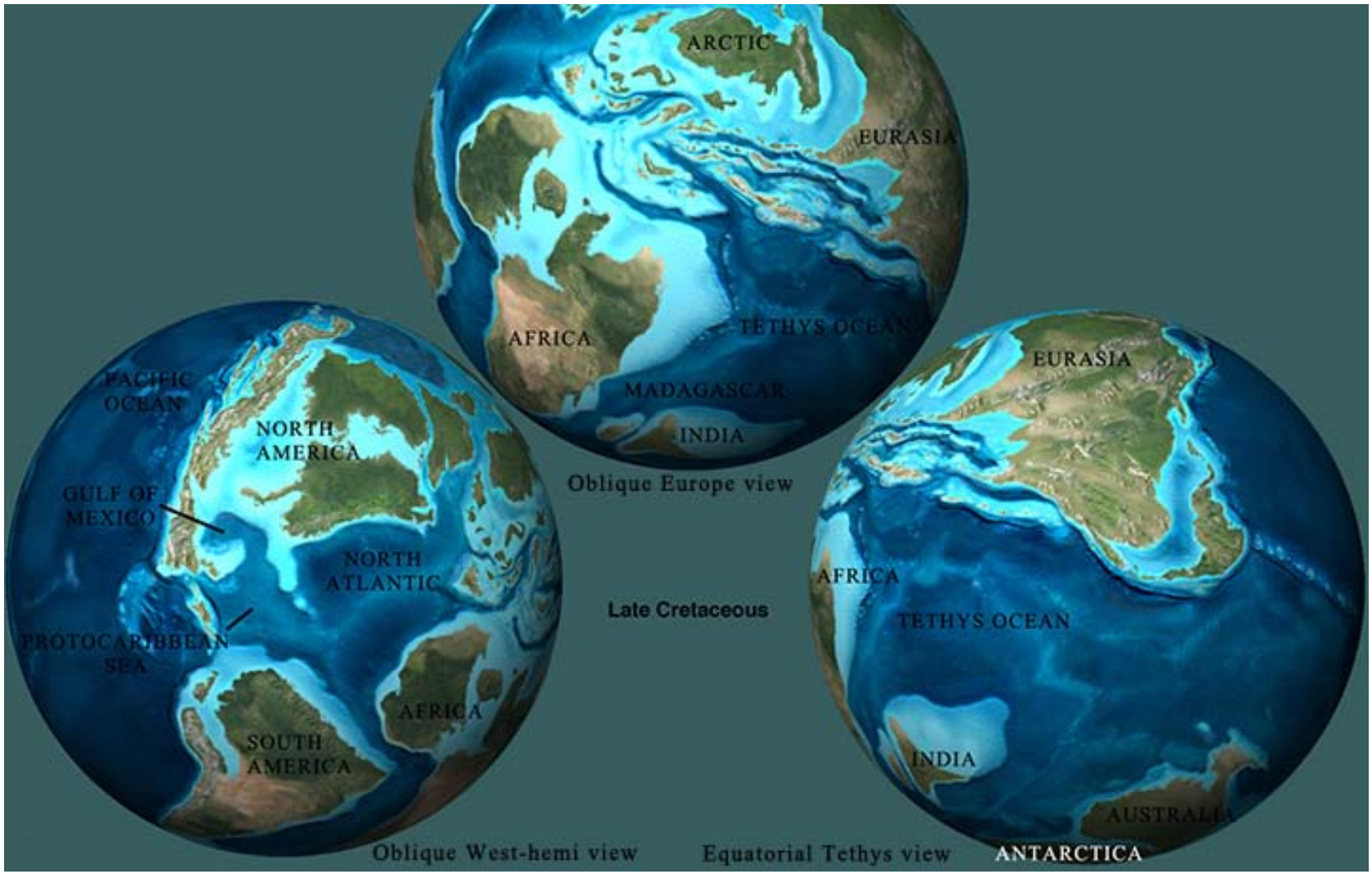

Figure 50. Paleogeographical reconstruction of the world during the late Cretaceous. North America is at approximately 45 degrees north latitude (After Blakey, 2009).

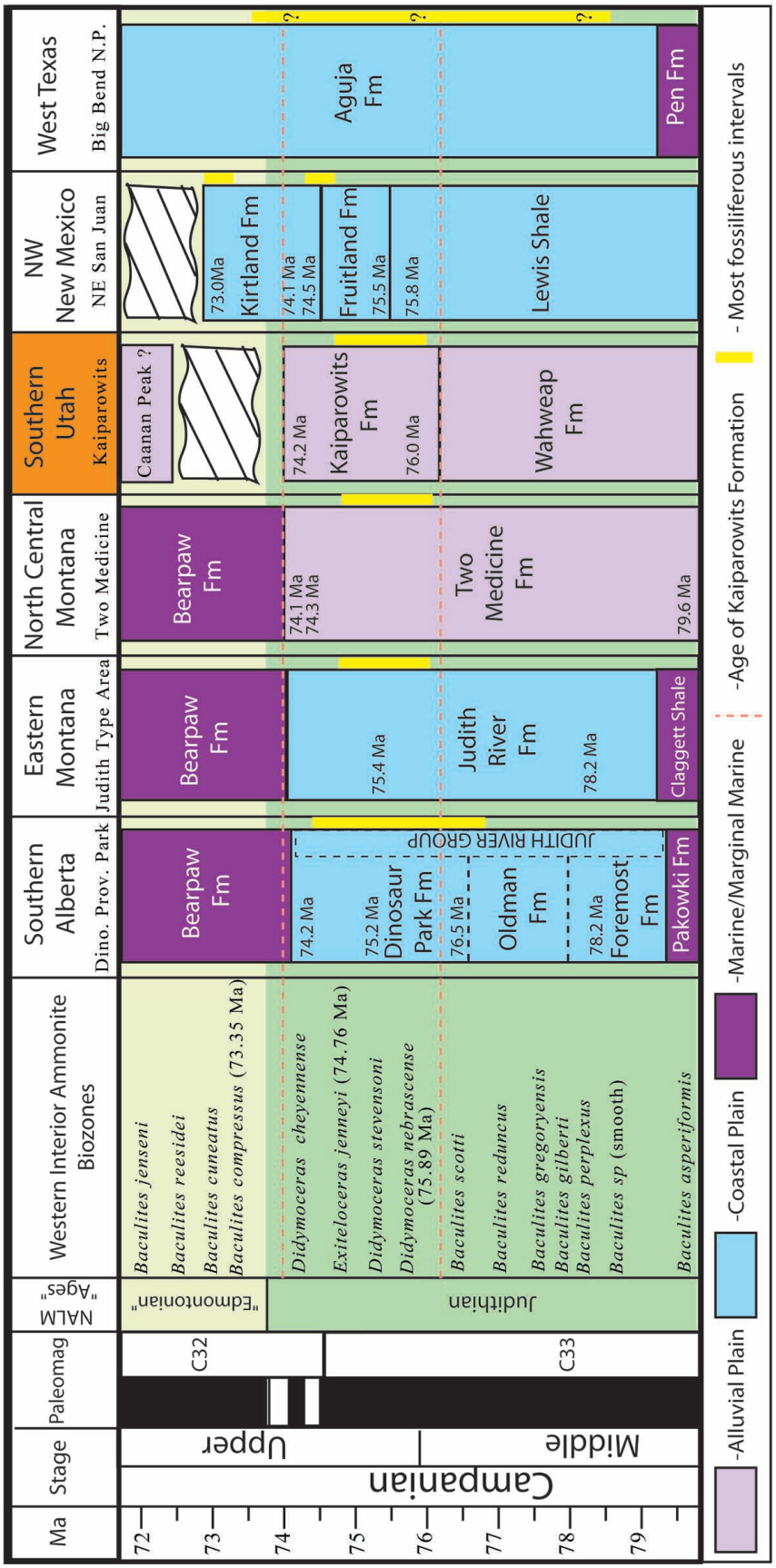

Figure 51. Correlation chart showing age relations of late Campanian strata in the WIB. Figure modified from Roberts et al. 2005.

Kaiparowits Formation and *Diabloceratops eatoni* from the underlying Wahweap Formation, challenge the long-held assumption that centrosaurines were rare or absent in the southern WIB (Lehman, 1997, 2001). *Diabloceratops* is the oldest known centrosaurine, dated at about 79 Ma (Jinnah et al., 2009) and thus predating *Nasutuceratops* by approximately 4 million years (Roberts et al., 2005; Roberts 2007). Morphologic data are consistent with the greater age of *Diabloceratops*, which possesses several plesiomorphic characters that are absent in *Nasutuceratops*; two examples are an accessory antorbital fenestra, otherwise present in the basal nonceratopsid neoceratopsians *Magnirostris* (IVPP V 12513) *Bagaceratops* (ZPAL MgD-I/126), and *Zuniceratops* (MSM P2101); and a relatively straight, nonexpanded ventral margin of the premaxilla (You and Dong, 2003; Maryanska and Osmólska , 1975; Wolfe and Kirkland, 1998). Interestingly, *Nasutuceratops* possesses several characters (e.g., rostrocaudally abbreviated maxilla, and near vertical caudal ramus of the premaxilla) which are present in some basal nonceratopsid neoceratopsians (e.g., *Leptoceratops*, NMC 8887; *Protoceratops*, AMNH 6425), but which are absent in *Diabloceratops*. The well supported placement of *Diabloceratops* at the base of Centrosaurinae (Fig. 48), combined with the relatively long snout present in the derived nonceratopsid neoceratopsian *Zuniceratops*, suggests that the facial skeleton of *Nasutuceratops* is secondarily (i.e., apomorphically) short and deep. Similarly, the elaborate epiparietal spikes present in *Diabloceratops* (Kirkland and DeBlieux, in press), and the predominance of elaborate epiparietal ornamentation in other centrosaurines, suggests that the simplified ornamentation condition present in *Nasutuceratops* may also be derived. If additional finds support these contentions, *Nasutuceratops* may represent the first example of a

previously unknown clade of late Campanian southern centrosaurines whose evolutionary trajectory was characterized by a significant restructuring of the facial skeleton.

The discovery of *Nasutuceratops* elucidates several evolutionary trends within Centrosaurinae (e.g., reduction in postorbital horncores; reduction of accessory antorbital fenestra, reorientation of the dorsal ascending ramus of the premaxilla; hypertrophy of the ventral margin of the premaxilla forming the characteristic ventral angle; reduction in ventral displacement of maxillary tooth row; and reduction in epijugal size). In particular, long, robust supraorbital ornamentation, once thought to be diagnostic of Chasmosaurinae, can now be regarded confidently as plesiomorphic for Ceratopsidae. The recent discovery of the long-horned basal centrosaurines *Albertaceratops* and *Diabloceratops*, now augmented by the younger *Nasutuceratops* described here, highlight the evolutionary trajectory of centrosaurines from long-horned forms to short-horned (e.g., *Centrosaurus*, *Einiosaurus*), and even bossed forms (e.g., *Achelousaurus*, *Pachyrhinosaurus*).

Similarly, the recent discoveries of *Diabloceratops*—which possesses the pliesiomorphic accessory antorbital fenestra, otherwise only present in basal nonceratopsid neoceratopsians (e.g., *Magnirostris*, IVPP V 12513; *Bagaceratops*, ZPAL MgD-I/126; and *Zuniceratops*, MSM P2101)— and *Nasutuceratops*, which lacks an accessory antorbital fenestra, highlights the evolutionary loss of this feature in more derived centrosaurines (e.g., *Centrosaurus*, *Pachyrhinosaurus*). Likewise, the discoveries of *Diabloceratops* and *Nasutuceratops* elucidate several evolutionary changes associated with the craniofacial skeleton within Centrosaurinae, including hypertrophy of the premaxilla in general, and the ventral margin in particular, forming the characteristic

ventral angle; reorientation of the dorsal ascending ramus of the premaxilla to become more horizontal in orientation; and reduction in ventral displacement of the maxillary tooth row. The characteristic ventral angle of the premaxilla is present in *Nasutuceratops* and northern centrosaurines, and it is absent from *Diabloceratops*. This supports the notion that *Nasutuceratops* and the northern centrosaurines shared a more recent common ancestor than either did with *Diabloceratops*. Ventral displacement of the maxillary tooth row is present in several basal nonceratopsid neoceratopsians (e.g., *Bagaceratops*, ZPAL MgD-I/126; *Magnirostris*, IVPP V 12513; and *Protoceratop*s, AMNH 6425), as well as the centrosaurines *Avaceratops* (ANSP 15800) and *Diabloceratops* (UMNH VP 16699), suggesting that the presence of this character state in *Nasutuceratops* (UMNH VP 16800) is sympliesiomorphic. The discoveries of *Diabloceratops* and *Nasutuceratops* from the late Campanian of Utah demonstrate a reduction in the size and shape of the epiossification associated with the jugal in centrosaurines, from a large epiossification to a small almost nonexistent epiossification.

The phylogenetic analysis of Centrosaurinae presented here (Fig. 48) provides key support for the hypothesis of late Campanian dinosaur provinciality in the WIB, indicating the presence of a northern clade of short-horned forms and a southern clade of long-horned forms that were geographically separated for almost 2 million years. In particular, the temporal overlap of *Centrosaurus apertus*, a typical short-horned, northern clade centrosaurine, and *Nasutuceratops titusi*, a long- horned, southern clade centrosaurine (Fig. 49), all but eliminates the alternative hypothesis that dinosaur provinciality is only apparent, the result of time-transgressive distribution of taxa (e.g., Sullivan and Lucas, 2006). Instead, the phylogenetic, stratigraphic, and biogeographic

evidence presented here is consistent with dinosaur provincialism, suggesting further that the two provinces served as independent evolutionary centers of endemism (Sampson and Loewen, in press).

Importantly, all centrosaurines other than *Nasutucertops* with elongate postorbital horncores (e.g., *Diabloceratops*, *Avaceratops*, and *Albertaceratops*) come from significantly older sediments (Fig. 49), making *Nasutuceratops* by far the latest occurring long-horned centrosaurine in the WIB. Given that derived northern centrosaurines (e.g., *Centrosaurus*, *Einiosaurus*, *Pachyrhinosaurus*) are likely descended from long-horned forms closely related to *Albertaceratops* (Ryan, 2007), the results presented here suggest that the centrosaurines in the southern and northern regions of the WIB may prove to be descended from independent branches arising from within the basal, long-horned radiation of centrosaurines.

CONCLUSION

Nasutuceratops titusi, recovered from the middle unit of the Kaiparowits Formation, represents a new basal centrosaurine from the late Campanian of southern Utah. *N. titusi* is distinguished from other centrosaurines by the possession of a rostrocaudally abbreviated and dorsoventrally deep preorbital region (e.g., short length to height ratio), highly pneumatized nasals, rostrocaudally narrow maxillae, hypertrophied premaxilla-maxilla contact; medially directed double faceted maxillary process contributing to a short, hard palette; and extremely elongate and robust supraorbital ornamentation. In contrast to virtually all other centrosaurines, the key diagnositc characters of *N. titusi* appear to be related not to structures of mate competition (i.e., horns and frills), but rather to the extreme shortening of the facial skeleton.

An in-depth phylogenetic analysis produced two most parsimonious trees of 264 steps, supporting the monophyly of Ceratopsidae, Centrosaurinae, and Chasmosaurinae. *Nasutuceratops titusi* is placed as the sister taxon to *Avaceratops lammersi* from the late Campanian of Montana. Two nonceratopsid neoceratopsians, *Turanoceratops* and *Zuniceratops*, fall out as respective sister taxa to Ceratopsidae. Bootstrap support for most clades in the strict consensus tree is relatively weak, with all clades but the Neoceratopsia and Chasmosaurinae being supported well below a 95% confidence level. Bremer support for the strict consensus tree is similarly weak. The lack of robustness in

the post-hoc tree statistics likely reflects the difficulty of establishing discrete and distinctive character states (particularly in the parietosquamosal frill) for most taxa.

Nasutuceratops elucidates and/or supports multiple evolutionary patterns within Centrosaurinae, including reduction in postorbital horncores; reduction of accessory antorbital fenestra; reorientation of the dorsal ascending ramus of the premaxilla; hypertrophy of ventral premaxillary margin, forming characteristic ventral angle and associated rostroventral trough; reduction in ventral displacement of maxillary tooth row; and reduction in epijugal size. Long, robust supraorbital ornamentation, once thought to be diagnostic of Ceratopsidae, can now be shown as plesiomorphic for the clade. The discoveries of *Diabloceratops* and *Nasutuceratops* from GSENM also elucidate the evolutionary loss of the accessory antorbital fenestra, a feature once thought to be restricted to basal nonceratopsid neoceratopsians. Additionally, *Nasutuceratops* highlights a reorientation of the craniofacial skeleton (e.g., reorientation of the dorsal ascending ramus of the premaxilla and maxilla) within centrosaurines, as well as the reduction in epijugal characterized by more derived forms.

Nasutuceratops is diagnosed by a relatively large number of autapomorphies that are unusual not only in terms of number but also of type. Most of these characters do not pertain to supraorbital and parietosquamosal frill ornamentation, but rather to aspects of the facial skeleton. This finding, coupled with the fact that *Nasutuceratops* is temporally much younger than other long-horned centrosaurines (e.g., *Avaceratops*, *Albertacertops*, and *Diabloceratops*), suggests that *Nasutuceratops* may represent a previously unknown radiation of short-snouted, long-horned centrosaurines in the southern WIB, differing from northern centrosaurine forms not only in supraorbital and frill ornamentation but

perhaps also in facial characters (i.e., short, deep preorbital facial skeleton). Whereas the latter are more likely to have evolved under the influence of sexual selection and other forces targeting mate signaling structures and reproductive success, the latter are more likely to be associated with evolution by natural selection and differential survival.

Biostratigraphically, *Nasutuceratops* is presently limited to the middle unit (~250-320 m) of the late Campanian Kaiparowits Formation, dated at ~75.9-75.2 Ma (Roberts et al., 2005; Roberts, 2007). This finding, coupled with the fact that *Nasutuceratops* is contemporaneous with *Centrosaurus* from the late Campanian of Alberta, provides robust support for late Campanian ceratopsid provincialism in the WIB.

Currently, ceratopsids represent one of the best documented clades of dinosaurs, with approximately 32 recognized species known from a relatively narrow temporal distribution. Recent discoveries from Alberta, Utah (this study), New Mexico, and Coahuila (Mexico) provide key insights into the mosaic evolution within ceratopsids generally and centrosaurs particularly. Long, robust supraorbital horncores are plesiomorphic within Ceratopsidae, and this study highlights the possibility that long snouts and highly adorned parietals are as well. Nevertheless, given the recent discoveries of multiple new ceratopsian taxa together with persistent temporal gaps in the existing fossil record of ceratopsids, it is inevitable that the diversity of horned dinosaurs in North America will continue to increase.

APPENDIX A

GLOSSARY OF TERMS

Analogous—features of different species that are similar in function but not necessarily in structure and evolved independently within the two species.

Anterior—directional term in anatomy (i.e., located near or toward the head).

Apomorphy—in cladistics, a derived or specialized character.

Autapomorphy—in cladistics, a derived trait that is unique to a given terminal group.

Caudal—directional term in anatomy (i.e., pertaining to the tail or hind part; equivalent to "posterior").

Clade—a group of organisms whose members share homologous (see below) features derived from a common ancestor.

Cladistics—hierarchial classification of species based on evolutionary ancestry.

Dorsal—directional term in anatomy (i.e., toward, on, or near the back or upper surface)

Eccentric—deviating from a circular form, having the axis located elsewhere than at the geometric center.

Ectonaris—the external bony aperture of the nasal cavity.

Ectonarial fossa—that portion of the narial fossa occurring immediately internal to the ectonaris and typically demarcated from the endonarial fossa by a pronounced bony ridge or strut.

Ectonarial recess—the recess within the premaxilla along the rostral margin of the ectonarial fossa, typically most developed rostroventrally.

Endonaris—the internal bony aperture of the nasal cavity which separates the nasal vestibule from the nasal cavity proper.

Endonarial fossa—that portion of the narial fossa surrounding the endonaris, varying considerably in relative size and extent within and among taxa. It is bound rostrally and ventrally by a faint ridge in centrosaurines.

Heterochrony—a developmental change in the timing of events, leading to changes in size and shape.

Holotype—the original specimen from which upon which the diagnosis of a new species is established.

Homologous—features of different species that originated from a common ancestor, and have the same typical structure and position, but not necessarily the same function.

Lateral—directional term in anatomy (i.e., relating to, or situated at or on the side).

Medial—directional term in anatomy (i.e., relating to, or situated at or toward the middle).

Monophyletic—in cladistics, a clade consisting of an ancestor and all of its descendants.

Narial fossa—the pronounced, bilateral depression in the snout bounded by the ectonaris and endonaris, and composed almost exclusively of premaxilla, with a small dorsal contribution from the nasal.

Narial spine—a distinct bony process that extends from the caudal ectonaril margin rostromedially into the nasal vestibule. This process, a derived feature of Centrosaurinae, arises from the nasal but often includes a ventral contribution from the premaxilla.

Nasal cavity proper—the main chamber of the nasal cavity.

Nasal vestibule—the outermost, rostrally placed chamber of the nasal cavity.

Nomen Dubium—a taxonomic name applied to an organism that is unknown or doubtful.

Ontogenetic—the origin and development of an individual organism from embryo to adult.

Paedomorphic—retention of juvenile characteristics in the adult form.

Parsimony—simplest explanation that explains the greatest number of observations.

Paucispecific—few or limited number of species.

Phylogeny—the sequence of events involved in the evolutionary development of a species or taxonomic group of organisms.

Plesiomorphy—in cladistics, an ancestral or primitive character.

Pneumatics—relating to cranial air-sacs or sinuses.

Provinciality—of or relating to a province, restricted to a particular geographical region.

Rostral—directional term in anatomy (i.e., situated toward a rostrum or toward the beak).

Symplesiomorphy—in cladistics, a character shared by a number of groups, but inherited from ancestors older than the last common ancestor.

Synapomorphy—in cladistics, an apomorphy (see above) shared by two or more groups that was present in their last common ancestor.

Ventral—directional term in anatomy (i.e., toward, on, or near the belly or lower surface).

APPENDIX B

CHARACTER LIST AND CHARACTER STATES

Character list and character states used to determine in group relationships of Centrosaurinae. The morphological characters utilized during this calibrated phylogeny are adapted from Sampson (1995), Ryan (2007), Currie et al., (2008), and Sampson et al., (unpublished data). The characters, where applicable, are listed as "new", and are unordered and unweighted. Basal condition (state) is assigned a numeric value of zero. References provided, represent authors who introduced, discussed, or modified the particular character.

DERMAL SKULL ROOF

1. Rostral, extent of dorsal and ventral processes (Dodson et al., 2004): triangular in lateral view, with short dorsal and ventral processes (0); elongate, with deeply concave caudal margin and hypertrophied dorsal and ventral processes (1).

2. Ectonaris and endonaris, size and position (Gregory & Mook, 1925; Brown and Schlaikjer, 1940a): small, restricted to dorsal 1/3 of premaxilla, ectonaris and endonaris undifferentiated, ectonaris length 10% or less that of basal skull length (0); large, ecto- and endonaris expanded to occupy most of the depth of the premaxilla, ectonaris differentiated from and much larger than endonaris, ectonaris 15% or greater than basal skull length (1).

3. Premaxillary septum (Forster, 1990): absent (0); present (1).

4. Premaxillary septum, shape: rostrally elongate (0); semicircular (1).

5. Premaxillary septum, nasal contribution: septum formed by premaxilla only (0); septum formed by premaxilla and nasal (1).

6. Premaxilla, narial strut (Forster et al., 1993): absent (0); present (1).

7. Premaxilla, narial strut orientation (Forster et al., 1993): rostrally inclined (0); caudally inclined (1).

8. Premaxilla, septal flange (Forster et al., 1993): absent (0); present (1).

9. Premaxilla, septal flange length (Forster et al., 1993): spans entire caudal margin of narial strut (0); restricted to ventral portion of narial strut (1).

10. Premaxilla, septal fossa (modified from Forster, 1996a): absent (0); present (1).

11. Premaxilla, septal fossa, septal recess (modified from Forster, 1996a): absent (0); present (1).

12. Premaxilla, accessory strut in septal fossa and septal recess (new): no accessory strut (0); strut present (1).

13. Premaxilla, endonarial process (Forster, 1990): absent (0); present (1).

14. Premaxilla, endonarial process shape (new): square (1); pinched and triangular with concave facets (1).

15. Premaxilla, endonarial process recess (Forster, 1990): absent (0); present (1).

16. Premaxilla, ectonarial recess (Sampson et al., in prep): absent (0); present (1).

17. Endonarial platform (new): absent (0); present (1).

18. Premaxilla, ventral angle (Forster, 1990): absent, (0); present, (1).

19. Premaxilla, ventral extent of caudoventral oral margin (bucal margin of Makovicky & Norell, 2006): above or at the level of alveolar margin of maxilla (0), expanded ventrally to extend well below alveolar margin of maxilla (1).

20. Premaxilla, position of caudal tip of caudoventral process (Forster et al., 1993): inserts into an embayment in the nasal (0); intervenes between nasal and maxilla (1).

21. Premaxilla, distal end of caudoventral process forked (Forster et al., 1993): absent (0); present (1).

22. Premaxilla-nasal contact in dorsal view (new): premaxilla slots into nasal (0); nasal slots into premaxilla (1).

23. Accessory antorbital fenestra (Kirkland and DeBlieux, in press): present (0); absent (1).

24. Accessory antorbital fenestra size (Kirkland and DeBlieux, in press): present pronounced, penetration of nasal cavity visible in lateral view (0); present, slight, nasal cavity not visible in lateral view (1).

25. Accessory antorbital fenestra nasal contribution (new): nasal contributes less than 60% of dorsal margin of AAOF (0); nasal contributes greater than 60% of dorsal margin of AAOF (1).

26. External antorbital fossa, size (Granger & Gregory, 1923; Chinnery & Weishampel, 1998): large, 20% or more length of body of maxilla (0); greatly reduced or absent, less than 10% length of body of maxilla (1).

27. Maxilla, tooth row (new): ventrally displaced from rostral edentulous portion of ventral surface of max (0); not ventrally displaced (1).

28. Maxilla, tooth row (new): rostral expansion of external surface of rostroventral surface of max (0); rostrolateral surface of maxilla not elongate (1).

29. Maxilla, maxillary cavity (Sampson et al., in prep): absent (0); present (1).

30. Maxilla, internal maxillary fossa (Sampson et al., in prep): absent (0); present (1).

31. Maxilla, length of alveolar process (Sereno, 1999): short, 25% or less (0); long, 30% or more length of toothrow (1).

32. Maxilla, ectotopterygoid/pterygoid complex (new): covers entire dorsal surface and laps onto lateral surface of caudal ramus of maxilla (0); ectopterygoid vestigial (1).

33. Nasal, ornamentation in adult (Forster, 1990): absent (0); present (1).

34. Nasal, ornamentation position, measured perpendicular to the toothrow (modified from Forster, 1990): centered dorsal to or caudal to center of endonaris (0); centered rostal to center of endonaris (1).

35. Nasal, epinasal ossification (Lehman, 1990; Forster, 1990): absent (0); present (1).

36. Nasal, dorsoventral thickness in midsaggital view (new): thin (0); thick (1).

37. Premaxilla, contribution to caudal margin of external naris: more than 50 percent (0); less than 50 percent (1).

38. Nasal, narial spine (Lehman, 1990; Forster, 1990): absent (0); present (1).

39. Facial skeleton, dorsoventral depth in orbital region (new): deep, caudal portion of maxilla entirely visible (0); shallow caudal portion of maxilla obscured by jugal (1).

40. Orbit, orientation: directed rostrolaterally (0); directed laterally (1).

41. Orbit diameter (Makovicky and Norell, 2006): more than 20% of skull length (0) or less (1).

42. Lacrimal, size (Brown and Schlaikjer, 1940a): large, forms 50% or more of the rostral orbital margin (0); small, forms 40% or less of the rostral orbital margin (1).

43. Postorbital, supraorbital ornamentation in adult: absent (0); present (1).

44. Postorbital, cornual sinuses in base of supraorbital ornamentation (Farke, 2006): absent (0); present (1).

45. Postorbital, extent of cornual sinuses in base of supraorbital ornamentation (Farke, 2006): sinus space invades frontal and parietal (0); sinus space enters postorbital (1).

46. Postorbital, type of subadult supraorbital ornamentation (Sampson, 1995): pointed apex, horncore at least as tall as long rostrocaudally (0); rounded apex, horncore longer rostrocaudally than high (1).

47. Postorbital, type of adult supraorbital ornamentation: horncore (0); rugose boss (1).

48. Postorbital, position of supraorbital horn (modified from Lehman, 1996): centered rostrodorsal or dorsal to orbit, narrow base with caudal margin of supraorbital horn extending to or only slightly behind caudal margin of orbit (0); centered caudodorsal to orbit, broad base with caudal margin of supraorbital horn extending well behind caudal orbit (1).

49. Postorbital, orientation of supraorbital horncore base (new): dorsally directed (0); dorsolaterally directed (1).

50. Postorbital, length of supraorbital horncore (Forster, 1990): short, less than 15% basal skull length (0); present, elongate, greater than 35% basal skull length (1).

51. Postorbital, curvature of supraorbital horncore in lateral view (modified from Forster et al., 1993): caudally recurved (0); rostrally curved (1); straight (2).

52. Postorbital, curvature of supraorbital horncore in rostral view (new): medially recurved (0); laterally curved (1); straight (2).

53. Prefrontal-prefrontal contact (Lambe, 1915; Forster, 1990): absent (0); present (1).

54. Palpebral, shape (Granger & Gregory, 1923): rod-like, articulates with prefrontal only at its base and projects across dorsal orbit, ligamentous attachment (0); blocky, fully fused into dorsal orbital margin, sutural articulation with prefrontal and frontal (1).

55. Palpebral, antorbital buttress (Ostrom and Wellnhofer, 1986; Sampson, 1995): absent (0); present (1).

56. Palpebral, extent of antorbital buttress (Ostrom and Wellnhofer, 1986; Sampson, 1995): present along only anteriodorsal portion of orbit (1); present along entire anterior portion of orbit (2).

57. Shape of jugal, broad D-shaped (0); narrow-waisted, T-shaped (1).

58. Jugal, size and orientation of jugal body: projects strongly caudoventrally, does not extend below the level of the maxillary tooth row (0); projects nearly ventrally, elongated to extend below the level of the maxillary tooth row (1).

59. Jugal infratemporal process (Brown and Schlaikjer, 1940a; Forster, 1990): absent (0); present, long contacts or nearly contacts infratemporal process of squamosal (1).

60. Epijugal attachment scar (new): large blade like triangle with obtuse angle oriented towards quadratojugal (0); scar roughly equilateral in shape (1).

61. Epijugal length (new): long (0); hyperlong (1); short (2).

62. Quadratojugal-squamosal contact (Brown and Schlaikjer, 1940a): absent (0); present (1).

63. Quadrate, exposure in lateral view (new): quadrate condyles not visible or slightly visible in lateral view (0); long, quadrate condyles fully visible in lateral view, extending ventral to jugal (1).

64. Laterotemporal fenestra, size and position (Brown and Schlaikjer, 1940a; Forster, 1990): relatively large, diameter 20% or greater that of basal skull length, positioned caudal to orbit (0); greatly reduced, diameter 10% or less that of basal skull length, positioned entirely below ventral limit of orbit (1).

65. Frontal, contribution to orbital margin (Brown and Schlaikjer, 1940a): present (0); absent (1).

66. Frontal, contribution to dorsotemporal fenestra (Lambe, 1915): present (0); absent (1).

67. Frontal fontanelle, shape (modified after Forster, 1996a): present, transversely narrow, slit-like (0); present, key-hole shaped, circular or elongate oval (1).

68. Parietal, anterior extent on dorsum of skull relative to occipital condyle: rostral end of parietal located well in front of occipital condyle (0); rostral end of parietal lies directly over occipital condyle (1).

69. Squamosal, shape of blade of squamosal (new): unexpanded laterally projecting rectangle (0); expanded and equilateral, subequal to square (1); caudally elongate (2).

70. Squamosal, length relative to parietal (new): squamosal unexpanded and does not contribute to lateral margin of frill (0); squamosal shorter than parietal with part of the lateral portion of the frill made up of parietal (1); squamosal equal or subequal to length to the parietal (2).

71. Squamosal forms part of posterior margin of frill (new): absent (0); present (1).

72. Squamosal, rostromedial lamina forming the caudolateral floor of dorsotemporal fossa (Dodson, 1986): absent (0); present (1).

73. Squamosal-quadrate contact (Hatcher et al., 1907; Forster, 1990): socket-like cotylus on ventrolateral squamosal for ball-like quadrate head (0); elongate groove on medial surface of squamosal to receive lamina of quadrate (1).

74. Squamosal, thickened, rounded swelling along medial margin (Forster, 1990; Farke, 2002: absent, lateral surface of squamosal flat to slightly convex (0); present, lateral surface of squamosal slightly concave (1).

75. Parietosquamosal contact, shape in lateral view (new): straight (0); curved, medially concave (1).

76. Parietal, concave median embayment on caudal edge of parietal (modified from Forster, 1990): absent or slight overall shape round (0); or very shallow medially restricted indentation (1); entire transverse bar is a shallow V-shaped embayment (2); present, pronounced, medially restricted notch-like embayment (3).

77. Parietal, location of caudalmost point of caudal ramus (Holmes et al., 2001): on midline (0); between midline and lateralmost corner (1); at lateralmost corner adjacent to squamosal (2).

78. Parietosquamosal frill, length relative to basal skull length (Hatcher et al., 1907; Lehman, 1990; Forster, 1990): short, .70 or less (0); elongate, .85 or more (1).

79. Parietosquamosal frill, location of maximum transverse width (new): caudally, at rear margin of frill (0); rostrally, in association with proximal half of frill (1); widest part in middle or frill relatively equal in width (2).

80. Parietal, parietal sulci (Marsh, 1892): absent (0); present or secondarily roofed over (1).

81. Parietal, overall shape: nearly straight along midline in lateral view and gently arched from side to side (0); "saddle-shaped," dorsally concave in lateral view with upturned caudal margin, and arched strongly from side to side (1).

82. Parietal fenestra (modified from Forster, 1990): no fenestra (0), present (1).

83. Parietal, rim on medial margin of dorsotemporal fenestra (Forster, 1990): absent (0); present, well-defined, laterally projecting rim defines medial margin of fenestra (1).

84. Parietal, sharp median crest (Sampson et al., 1997): present (0); absent (1).

85. Parietal, rostrocaudal thickness of transverse bar at narrowest point (modified from Forster et al., 1993): narrow and straplike, less than 10% total parietal length (0); broad, 20% or more of total parietal length (1).

86. Parietal, relative rostrocaudal depth of broad transverse bar (new): subequal medial to lateral (0); tapering medially (1).

87. Parietal, cross-sectional shape of median bar (Holmes et al., 2001): triangular, tapers laterally (0); rectangular or subrectangular with a facet, margin facing parietal fenestrae thick and oriented sub-perpendicular to parietal surface (1); round to lenticular (2); v-shaped without thickening (3).

88. Parietal, median bar, transverse width (Holmes et al., 2001): narrow and straplike, transverse width less than 10% total parietal length (0); relatively wide, transverse width 15% or more of total parietal length (1).

89. Parietal fenestra, orientation (Forster, 1990): long axis directed transversely (1); long axis directed axially (2); axial and transverse axes equal (3).

90. Parietal fenestra, maximum proximodistal diameter (adapted from Forster et al., 1993): 35% or less total parietal length (0); 45% or more total parietal length (1).

91. Parietosquamosal frill, marginal undulations (Gilmore, 1917): absent (0); present (1).

92. Parietosquamosal frill, imbrication of undulations (Sampson et al, 1997): absent (0); present (1).

EPIOSSIFICATIONS

93. Marginal dermal ossifications on parietal and squamosal: absent (0); present (1).

94. Episquamosals on midlateral squamosal margin (new): small, less than 50 mm long in adults (0); large and elongate, greater than 90mm long in adults (1).

95. Episquamosal, location of largest example (new); episquamosals subequal in size (0); rostralmost episquamosal by far the largest (1); caudalmost episquamosal by far the largest proximodistally relative to other episquamosals on this element (2).

96. Midlateral episquamosal, shape (new): crescentic or ellipsoidal (0); triangular or elongate (1).

97. Number of episquamosals on squamosal (new): three to five episquamosals (0); six or more episquamosals (1).

98. Episquamosal shape at locus S1, most caudal (new): small and crescentic (0); low raised D-shaped process (1); well developed larger triangular process (2); elongate hook (3);

99. Episquamosal shape at locus S2, second most caudal (new): small and crescentic (0); low raised D-shaped process (1); well developed larger triangular process (2); elongate hook (3);

100. Relative size and shape episquamosal locus S2, second most caudal (new): subequal to adjacent episquamosals (0); large well developed triangular process second only to S1 in size (1).

101. Marginal ossification crossing squamosal-parietal contact EPS1 (new): absent (0); present (1).

102. Epiparietal-squamosal shape at locus SP1 (new): small and crescentic (0); present strongly recurved process or gnarled process (1); well developed triangular process sometimes with a small peak (2).

103. Epiparietals, number per side (new): three (0); five or more (1).

104. Epiparietals, fused to adjacent epiparietal at base (modified from Holmes et al., 2001): absent (0); present (1).

105. Epiparietal P0 on caudal midline of frill (new): absent on caudal midline (0); present on caudal midline (1).

106. Epiparietal locus DPP1 (new): absent (0); present (1).

107. Shape of epiparietal locus P1 (new): low D-shaped process (0); elongate flattened process or spike (1), strongly recurved triangular or recurved low gnarled triangular process (2); well developed triangular process (3); elongate low process sometimes with a small peak (4).

108. Epiparietal, orientation at locus P1 (new): caudally, epiparietal oriented in the plane of the frill (0); directed rostrodorsally (1).

109. Epiparietal, curvature at locus P1 (new): straight (0); laterally curved (1); medially curved (2); recurved onto dorsal surface of frill (3).

110. Shape of epiparietal locus P2 (new):): low D-shaped process (0); elongate flattened process or spike (1), strongly recurved triangular or recurved low gnarled triangular process (2); well developed triangular process (3); elongate low process sometimes with a small peak (4).

111. Epiparietal, curvature at locus P2 (new): straight (0); medially or laterally curved in the plane of the frill (1); recurved onto dorsal surface of frill (2).

112. Shape of epiparietal locus P3 (new): low raised D-shaped process (0); elongate spike (1); strongly recurved triangular or recurved low gnarled triangular process (2); well developed triangular process (3); elongate low process sometimes with a small peak (4).

113. Epiparietal, orientation at locus P3 (new): caudally, epiparietal oriented in the plane of the frill (0); directed rostrodorsally (1).

114. Epiparietal locus P4 (new): absent (0); present (1).

115. Epiparietal shape at locus P4 (new): low process (0); elongate spike (1).

116. Epiparietal locus P5 (new): absent (0); present (1).

117. Epiparietal shape at locus P5 (new): D-shaped or triangular process (0); elongate spike (1).

118. Epiparietal locus P6 (new): absent (0); present (1).

BRAINCASE

119. Basioccipital,contribution to occipital condyle (Brown and Schlaikjer, 1940a): forms approximately 2/3 of occipital condyle (0); forms 1/3 of the occipital condyle (1).

120. Olfactory nerve (CN I), frontal contribution to exit from braincase (Forster, 1990): present, frontal forms roof of olfactory tract (0); absent, olfactory tract enclosed entirely by ossification of the laterospenoid (1).

121. Supraoccipital, contribution to foramen magnum (Brown and Schlaikjer, 1940a): forms dorsal margin of foramen magnum (0); eliminated from margin by exoccipital-exoccipital contact on midline (1).

122. Supraoccipital, ventrolateral processes (Brown and Schlaikjer, 1940a): absent (0); present (1).

123. Supraoccipital, ventrolateral processes, arcuate dorsolateral ridge between midline superoccipital ridge and top of exoccipital wing (new): present (0); absent (1).

124. Exoccipital, exits for cranial nerves in exoccipital (Brown and Schlaikjer, 1940a; Forster, 1990): three foramina (0); two foramina (1).

125. Paroccipital process, dorsoventral distal expansion (Brown and Schlaikjer, 1940a): distal process only slightly expanded (0); distal process expanded to at least .8 two times the depth at its narrowest point (1).

PALATE

126. Ectopterygoid contributes to palate and contacts the jugal (Brown and Schlaikjer, 1940a): present (0); absent (1).

127. Palatomaxillary foramen (Hatcher et al., 1907): absent (0); present (1).

128. Vomer, relationship to maxillae on secondary palate (Brown and Schlaikjer, 1940a): vomers insert between maxillae at the rear of the secondary palate (0); vomers meet caudal margin of maxillae on secondary palate, do not insert between maxillae (1)

129. Secondary palate, relative contribution of maxilla (Brown and Schlaikjer, 1940a): maxilla forms at least 45% of the secondary palate (0); maxilla contributes only to the posterior portion, forms 30% or less of secondary palate (1).

130. Palatine, shape and relationship to maxilla (Osmólska, 1986): palatine contacts nearly the entire medial surface of the maxilla, restricting size of choanae, rostrodorsal process embraces posterior end of vomer (0); palatine contacts only the posterior one-third of medial surface of maxilla, contact with vomer lost, choanae enlarged (1).

LOWER JAW

131. Lower jaw, level of mandibular articulation (Ostrom, 1964; Forster, 1990): at or slightly below occlusal surface of tooth row (0); depressed well below level of occlusal surface of tooth row (1).

132. Predentary, dentary processes: ventral processes much longer than abbreviated dorsal processes (0); dorsal and ventral processes elongate and subequal in length (1).

133. Predentary, orientation of triturating surface (Lehman, 1990; Forster, 1990): nearly horizontal (0); inclined steeply laterally (1).

134. Dentary lateral ridge confluent with cutting surface of predentary. present (0); absent (1).

135. Dentary rostroventral cavity below lateral ridge (new): absent (0), present (1).

136. Dentary rostroventral cavity below lateral ridge size (new): deep (0); weakly present (1).

137. Dentary, shape of ventral margin in adults (Brown and Schlaikjer, 1940a): strongly convexly bowed (0); straight (1).

138. Dentary, caudal extent of tooth row (Brown and Schlaikjer, 1940a): terminates at the center of the coronoid process (0); terminates caudal to the coronoid process (1).

139. Dentary, shape of coronoid process (Lull, 1933): short, with gently convex apex, base of ascending ramus rostrocaudally expanded (0); tall, expanded at apex into a rostrally projecting hook, base of ascending ramus rostrocaudally restricted (1).

140. Dentary, separation of body from ascending ramus of coronoid process (Granger & Gregory, 1923): absent (0); present (1

141. Splenial, shape (Brown and Schlaikjer, 1940a, 1940b): nearly as deep as the body of the dentary, does not contact articular, angular exposed in medial view (0); shallow, contacts articular, covers angular in medial view (1).

142. Coronoid bone, size (Brown and Schlaikjer, 1940a, 1940b): large, contacts the splenial (0); small, splenial process lost (1).

143. Angular, exposure in lateral view (Brown and Schlaikjer, 1940a): extensive (0); greatly restricted (1).

144. Surangular dorsally projecting ridge on lateral margin; present (0); absent (1)

145. Prearticular-dentary contact (Brown and Schlaikjer, 1940a, 1940b): absent (0); present (1).

146. Articular, size and contribution to mandibular glenoid (Brown and Schlaikjer, 1940a): articular forms only the medial 1/3 of the articular surface, extends caudally as far as the angular (0); articular enlarged, forms half of the articular surface, extends behind angular to form rear of lower jaw (1).

DENTITION

147. Tooth, number of roots: one (0); two (1).

148. Premaxillary teeth (new): absent90); present (1).

149. Tooth, number of replacements per alveolus: one or two replacement teeth (0); three or more replacement teeth (1).

150. Tooth magazine, case-like alveolar slots for vertical tooth families formed by spongy bone (Brown & Schlaijker, 1940a): absent (0); present (1).

PECTORAL GIRDLE AND LIMB

151. Scapula, relative contribution to glenoid fossa (Brown and Schlaikjer, 1940a): scapula and coracoid contribute equally (0); scapula contributes well over half of the glenoid (1).

152. Scapula, orientation of scapular spine: runs obliquely across blade (0); runs longitudinally along blade (1).

153. Clavicle: present (0); absent (1).

154. Humerus, length of deltopectoral crest in adult (Chinnery, 2004): short, less than 40% total humeral length (0); elongate, subequal to or greater than 45% of the total humeral length (1).

155. Ulna, size of olecranon process (Adams, 1988): moderately tall, occupies 32% or less total length of ulna (0); high, occupies at least 40% total length of ulna (1).

APPENDIX C

CHARACTER STATE MATRIX

taxon	1	2	3	4	5	6	7	8	9	10
Leptoceratops gracilis	1	0	2	0	-	-	0	-	-	-
Bagaceratops rozhdestvenskyi	0	0	1	0	-	-	0	-	-	-
Magnirostris dodsoni	0	0	1	0	-	-	0	-	-	-
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	?	?
Protoceratops andrewsi	0	0	2	0	-	-	0	-	-	-
Zuniceratops christopheri	1	1	?	1	0	0	0	-	-	-
Diabloceratops eatoni	0	1	0	1	1	1	0	-	-	-
Albertaceratops nesmoi	?	1	0	1	1	?	0	-	-	-
Nasutuceratops titusi	0	1	0	1	1	1	0	-	-	-
Avaceratops lammersi	0	1	0	1	1	?	0	-	-	-
Centrosaurus apertus	0	1	0	1	1	1	0	-	-	-
Centrosaurus brinkmani	0	1	0	1	1	1	0	-	-	-
Rubeosaurus ovatus	0	1	?	1	1	?	0	-	-	-
Styracosaurus albertensis	0	1	0	1	1	1	0	-	-	-
Einiosaurus procurvicornis	?	1	0	1	1	1	0	-	-	-
Achelousaurus horneri	0	1	0	1	1	1	0	-	-	-
Pachyrhinosaurus canadensis	0	1	0	1	1	1	0	-	-	-
Pachyrhinosaurus lakustai	0	1	0	1	1	1	0	-	-	-
Chasmosaurus belli	1	1	0	1	0	0	1	0	1	0
Chasmosaurus russelli	1	1	0	1	0	0	1	0	1	0
Chasmosaurus kaiseni	1	1	0	1	0	0	1	0	1	1
Pentaceratops sternbergi	1	1	0	1	0	0	1	0	1	1
Triceratops horridus	1	1	0	1	0	0	1	0	0	-

taxon	11	12	13	14	15	16	17	18	19	20
Leptoceratops gracilis	0	-	-	0	-	-	0	0	1	0
Bagaceratops rozhdestvenskyi	0	-	-	0	-	-	0	0	1	0
Magnirostris dodsoni	0	-	-	0	-	-	0	0	1	0
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	?	?
Protoceratops andrewsi	0	-	-	0	-	-	0	0	1	0
Zuniceratops christopheri	0	-	-	0	-	-	0	0	?	?
Diabloceratops eatoni	0	-	-	0	-	-	0	1	1	0
Albertaceratops nesmoi	0	-	-	0	-	-	?	?	?	?
Nasutuceratops titusi	0	-	-	0	-	-	1	1	1	1
Avaceratops lammersi	0	-	-	0	-	-	0	0	1	1
Centrosaurus apertus	0	-	-	0	-	-	1	1	1	1
Centrosaurus brinkmani	0	-	-	0	-	-	1	?	1	1
Rubeosaurus ovatus	0	-	-	0	-	-	1	1	1	?
Styracosaurus albertensis	0	-	-	0	-	-	1	1	1	1
Einiosaurus procurvicornis	0	-	-	0	-	-	1	?	?	?
Achelousaurus horneri	0	-	-	0	-	-	1	?	1	1
Pachyrhinosaurus canadensis	0	-	-	0	-	-	1	1	1	1
Pachyrhinosaurus lakustai	0	-	-	0	-	-	1	1	1	1
Chasmosaurus belli	1	0	0	1	0	0	0	0	0	0
Chasmosaurus russelli	1	0	0	1	0	0	0	0	0	0
Chasmosaurus kaiseni	1	0	0	1	0	0	0	0	0	0
Pentaceratops sternbergi	1	0	0	1	1	0	0	0	0	0
Triceratops horridus	1	1	1	1	1	1	0	0	0	0

taxon	21	22	23	24	25	26	27	28	29	30
Leptoceratops gracilis	1	0	0	0	1	1	-	-	0	0
Bagaceratops rozhdestvenskyi	0	0	0	0	1	0	0	0	0	0
Magnirostris dodsoni	0	0	0	0	1	0	0	0	0	0
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	0	0
Protoceratops andrewsi	0	0	0	0	1	0	1	0	0	0
Zuniceratops christopheri	?	0	1	0	?	0	0	1	0	?
Diabloceratops eatoni	0	0	0	1	0	0	0	1	0	0
Albertaceratops nesmoi	?	?	?	0	0	1	-	-	1	0
Nasutuceratops titusi	1	1	0	0	0	1	-	-	1	0
Avaceratops lammersi	1	?	0	?	0	1	?	?	1	0
Centrosaurus apertus	1	1	0	0	0	1	-	-	1	1
Centrosaurus brinkmani	1	?	?	0	0	1	-	-	1	1
Rubeosaurus ovatus	1	?	?	0	0	?	?	?	?	?
Styracosaurus albertensis	1	1	0	0	0	1	-	-	1	1
Einiosaurus procurvicornis	?	?	?	?	0	1	-	-	1	1
Achelousaurus horneri	1	1	0	?	0	1	-	-	1	1
Pachyrhinosaurus canadensis	1	?	0	?	0	1	-	-	1	1
Pachyrhinosaurus lakustai	1	1	0	0	0	1	-	-	1	1
Chasmosaurus belli	-	0	1	0	0	0	1	0	1	1
Chasmosaurus russelli	-	0	1	0	0	0	1	0	1	1
Chasmosaurus kaiseni	-	0	1	0	0	0	0	0	0	1
Pentaceratops sternbergi	-	0	1	1	0	0	1	0	1	1
Triceratops horridus	-	1	0	0	0	1	-	-	1	1

taxon	31	32	33	34	35	36	37	38	39	40
Leptoceratops gracilis	0	?	?	1	0	0	-	-	0	0
Bagaceratops rozhdestvenskyi	0	0	0	0	0	1	0	0	0	0
Magnirostris dodsoni	0	?	?	0	0	1	0	0	0	0
Turanoceratops tardabilis	0	0	0	?	0	?	?	?	?	?
Protoceratops andrewsi	0	0	0	0	0	1	0	0	0	0
Zuniceratops christopheri	0	0	0	1	0	0	-	-	0	0
Diabloceratops eatoni	0	?	?	1	0	1	0	0	?	1
Albertaceratops nesmoi	1	1	0	1	?	1	0	0	0	?
Nasutuceratops titusi	0	1	0	1	0	1	0	0	0	0
Avaceratops lammersi	0	1	1	1	?	?	?	?	?	?
Centrosaurus apertus	1	1	0	1	1	1	1	0	0	1
Centrosaurus brinkmani	1	1	0	1	1	1	1	0	0	1
Rubeosaurus ovatus	?	?	?	?	?	?	1	0	?	?
Styracosaurus albertensis	1	1	0	1	1	1	1	0	0	1
Einiosaurus procurvicornis	1	1	0	1	1	1	1	0	0	1
Achelousaurus horneri	1	1	0	1	1	1	2	0	0	?
Pachyrhinosaurus canadensis	1	1	0	1	1	1	2	0	0	0
Pachyrhinosaurus lakustai	1	1	0	1	1	1	2	0	0	0
Chasmosaurus belli	1	1	1	1	1	1	1	0	1	1
Chasmosaurus russelli	1	1	1	1	1	1	1	0	1	1
Chasmosaurus kaiseni	1	?	?	1	1	1	1	0	?	1
Pentaceratops sternbergi	1	1	1	1	1	1	1	0	1	1
Triceratops horridus	1	1	1	1	1	1	1	1	1	1

taxon	41	42	43	44	45	46	47	48	49	50
Leptoceratops gracilis	0	0	0	0	0	0	-	-	-	-
Bagaceratops rozhdestvenskyi	0	0	0	0	0	0	-	-	-	-
Magnirostris dodsoni	0	0	0	0	0	1	0	-	?	0
Turanoceratops tardabilis	?	?	?	1	?	1	0	-	?	0
Protoceratops andrewsi	0	0	0	0	0	0	0	-	-	-
Zuniceratops christopheri	0	?	1	1	1	1	1	0	0	0
Diabloceratops eatoni	1	0	1	1	1	1	?	?	?	0
Albertaceratops nesmoi	?	?	1	1	?	1	?	?	?	0
Nasutuceratops titusi	1	0	1	1	1	1	1	1	?	0
Avaceratops lammersi	1	?	?	1	?	?	?	?	?	?
Centrosaurus apertus	1	0	1	1	1	1	1	0	0	0
Centrosaurus brinkmani	1	?	1	1	1	1	1	0	0	0
Rubeosaurus ovatus	?	?	?	1	?	1	1	0	0	0
Styracosaurus albertensis	1	0	1	1	1	1	1	0	0	0
Einiosaurus procurvicornis	1	?	1	1	1	1	1	1	1	0
Achelousaurus horneri	1	?	1	1	1	1	1	1	1	1
Pachyrhinosaurus canadensis	1	0	1	1	1	1	1	1	?	1
Pachyrhinosaurus lakustai	1	0	1	1	1	1	1	1	1	1
Chasmosaurus belli	0	1	1	1	1	1	1	1	?	0
Chasmosaurus russelli	0	1	1	1	1	1	1	1	?	0
Chasmosaurus kaiseni	0	0	1	1	1	1	1	1	?	0
Pentaceratops sternbergi	0	0	1	1	1	1	1	1	?	0
Triceratops horridus	0	0	1	1	1	1	1	1	0	0

taxon	51	52	53	54	55	56	57	58	59	60
Leptoceratops gracilis	-	-	-	-	-	-	0	0	0	-
Bagaceratops rozhdestvenskyi	-	-	-	-	-	0	0	0	0	-
Magnirostris dodsoni	0	0	0	-	-	0	0	0	0	-
Turanoceratops tardabilis	0	0	1	-	1	?	?	1	?	?
Protoceratops andrewsi	-	-	-	-	-	0	0	0	0	-
Zuniceratops christopheri	0	0	1	0	2	1	?	1	1	0
Diabloceratops eatoni	0	0	1	0	2	1	?	1	1	0
Albertaceratops nesmoi	0	0	1	1	2	1	?	1	1	1
Nasutuceratops titusi	0	1	1	?	0	1	?	1	1	0
Avaceratops lammersi	?	?	?	?	?	1	?	?	?	?
Centrosaurus apertus	0	0	0	2	1	1	1	1	1	1
Centrosaurus brinkmani	0	1	0	2	1	1	1	1	1	1
Rubeosaurus ovatus	0	0	0	-	-	1	?	1	?	?
Styracosaurus albertensis	0	0	-	-	-	1	1	1	1	1
Einiosaurus procurvicornis	0	0	-	-	-	1	0	1	0	-
Achelousaurus horneri	0	0	-	-	-	1	?	1	0	-
Pachyrhinosaurus canadensis	1	-	-	-	-	1	?	1	0	-
Pachyrhinosaurus lakustai	1	-	-	-	-	1	?	1	0	-
Chasmosaurus belli	0	0	0	0	2	1	0	1	1	1
Chasmosaurus russelli	0	0	0	0	2	1	?	1	1	1
Chasmosaurus kaiseni	0	1	1	0	0	1	?	1	1	1
Pentaceratops sternbergi	0	0	1	1	2	1	0	1	1	1
Triceratops horridus	1	0	1	1	2	1	0	1	1	1

taxon	61	62	63	64	65	66	67	68	69	70
Leptoceratops gracilis	0	0	0	0	0	0	0	0	0	0
Bagaceratops rozhdestvenskyi	0	0	0	0	0	0	0	0	0	0
Magnirostris dodsoni	0	0	0	0	0	0	0	0	0	0
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	?	?
Protoceratops andrewsi	0	0	0	0	0	0	0	0	0	0
Zuniceratops christopheri	0	1	1	?	?	0	?	?	?	1
Diabloceratops eatoni	1	1	1	1	1	0	0	1	1	1
Albertaceratops nesmoi	0	1	1	1	1	1	2	1	1	1
Nasutuceratops titusi	?	?	?	1	1	1	0	?	?	1
Avaceratops lammersi	0	1	0	?	?	?	?	?	1	1
Centrosaurus apertus	0	1	1	1	1	1	2	1	1	1
Centrosaurus brinkmani	0	1	1	1	1	1	2	1	?	1
Rubeosaurus ovatus	?	?	?	?	?	?	?	?	?	?
Styracosaurus albertensis	0	1	1	1	1	1	2	1	1	1
Einiosaurus procurvicornis	0	1	1	1	1	1	2	1	?	1
Achelousaurus horneri	0	1	?	1	1	1	2	1	?	1
Pachyrhinosaurus canadensis	0	1	1	1	1	1	2	1	1	1
Pachyrhinosaurus lakustai	0	1	?	1	1	1	2	?	?	1
Chasmosaurus belli	0	1	1	1	1	1	2	1	0	1
Chasmosaurus russelli	0	1	1	1	1	1	2	1	0	1
Chasmosaurus kaiseni	1	1	1	1	1	1	0	1	0	1
Pentaceratops sternbergi	1	1	0	1	1	1	1	1	1	1
Triceratops horridus	1	1	0	1	1	1	2	1	0	1

taxon	71	72	73	74	75	76	77	78	79	80
Leptoceratops gracilis	0	0	0	-	0	0	0	1	0	0
Bagaceratops rozhdestvenskyi	0	0	0	-	0	0	0	?	?	?
Magnirostris dodsoni	0	0	0	-	0	?	?	?	?	?
Turanoceratops tardabilis	1	?	0	-	?	?	?	?	?	?
Protoceratops andrewsi	0	0	0	-	0	0	0	0	1	0
Zuniceratops christopheri	1	?	?	?	?	?	?	?	?	0
Diabloceratops eatoni	1	1	1	0	0	0	1	0	1	1
Albertaceratops nesmoi	1	?	?	?	1	1	1	0	1	1
Nasutuceratops titusi	1	1	1	0	1	1	1	0	1	1
Avaceratops lammersi	?	?	?	?	?	1	1	0	0	1
Centrosaurus apertus	1	1	1	0	1	1	1	0	1	1
Centrosaurus brinkmani	1	1	1	0	1	1	1	0	1	1
Rubeosaurus ovatus	?	?	?	?	?	?	?	0	?	?
Styracosaurus albertensis	1	1	1	0	1	1	1	0	1	1
Einiosaurus procurvicornis	1	1	1	0	1	1	1	0	1	1
Achelousaurus horneri	1	?	1	0	1	1	1	0	1	1
Pachyrhinosaurus canadensis	1	?	1	0	1	?	?	?	1	1
Pachyrhinosaurus lakustai	1	1	1	0	1	1	1	0	1	1
Chasmosaurus belli	1	1	1	1	1	2	1	0	0	1
Chasmosaurus russelli	1	1	1	1	1	2	1	0	0	1
Chasmosaurus kaiseni	1	1	1	1	1	2	1	0	0	?
Pentaceratops sternbergi	1	1	1	1	1	2	2	0	0	1
Triceratops horridus	1	1	2	1	1	2	2	0	0	1

taxon	81	82	83	84	85	86	87	88	89	90
Leptoceratops gracilis	0	0	0	0	0	0	0	0	0	0
Bagaceratops rozhdestvenskyi	?	0	0	0	0	?	0	?	?	?
Magnirostris dodsoni	?	?	?	?	?	?	?	?	?	?
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	?	?
Protoceratops andrewsi	0	0	0	0	0	0	0	0	1	0
Zuniceratops christopheri	?	?	?	?	?	?	?	0	1	?
Diabloceratops eatoni	0	0	3	1	1	1	1	0	1	1
Albertaceratops nesmoi	0	0	1	1	1	1	1	0	1	1
Nasutuceratops titusi	0	0	0	1	1	?	1	0	1	1
Avaceratops lammersi	0	0	0	0	1	2	?	0	0	?
Centrosaurus apertus	0	0	1	1	1	0	1	0	1	1
Centrosaurus brinkmani	0	0	1	1	1	0	1	0	1	1
Rubeosaurus ovatus	?	?	1	?	?	?	?	?	?	1
Styracosaurus albertensis	0	0	1	1	1	0	1	0	1	1
Einiosaurus procurvicornis	0	0	1	1	1	0	1	0	1	1
Achelousaurus horneri	0	0	1	1	1	0	1	0	1	1
Pachyrhinosaurus canadensis	0	0	?	1	1	0	1	0	1	?
Pachyrhinosaurus lakustai	0	0	1	1	1	0	1	0	1	1
Chasmosaurus belli	1	1	2	2	1	0	1	0	1	0
Chasmosaurus russelli	1	1	3	1	1	0	1	0	1	0
Chasmosaurus kaiseni	1	1	3	1	1	0	0	0	1	0
Pentaceratops sternbergi	1	1	3	2	1	1	1	0	1	1
Triceratops horridus	0	1	0	0	0	2	1	1	0	0

taxon	91	92	93	94	95	96	97	98	99	100
Leptoceratops gracilis	0	-	-	-	-	-	?	0	0	0
Bagaceratops rozhdestvenskyi	0	?	?	?	?	?	?	?	?	0
Magnirostris dodsoni	?	?	?	?	?	?	?	?	?	?
Turanoceratops tardabilis	?	?	?	?	?	?	?	1	?	?
Protoceratops andrewsi	0	0	0	0	0	1	0	0	0	0
Zuniceratops christopheri	0	1	0	0	0	?	?	?	?	0
Diabloceratops eatoni	1	1	0	0	1	2	1	1	1	1
Albertaceratops nesmoi	1	1	0	0	1	2	1	1	1	1
Nasutuceratops titusi	1	1	0	0	1	2	1	1	0	1
Avaceratops lammersi	1	-	-	-	-	-	-	1	0	?
Centrosaurus apertus	1	1	0	0	1	2	1	1	1	1
Centrosaurus brinkmani	1	1	0	0	1	2	1	1	1	1
Rubeosaurus ovatus	?	?	0	?	1	2	?	?	?	1
Styracosaurus albertensis	1	1	0	0	1	2	1	1	1	1
Einiosaurus procurvicornis	1	1	0	0	1	2	1	1	1	1
Achelousaurus horneri	1	1	0	0	1	2	1	1	1	1
Pachyrhinosaurus canadensis	1	?	?	0	?	?	1	1	1	?
Pachyrhinosaurus lakustai	1	1	0	0	1	2	1	1	1	1
Chasmosaurus belli	1	0	0	1	0	2	1	1	0	1
Chasmosaurus russelli	1	0	0	1	0	2	1	1	0	1
Chasmosaurus kaiseni	1	0	0	2	0	2	1	1	0	1
Pentaceratops sternbergi	1	0	1	2	0	2	1	1	0	1
Triceratops horridus	1	-	-	-	-	-	-	1	0	1

taxon	101	102	103	104	105	106	107	108	109	110
Leptoceratops gracilis	-	-	-	-	-	-	-	-	-	-
Bagaceratops rozhdestvenskyi	-	-	-	-	-	-	-	-	-	-
Magnirostris dodsoni	?	?	?	?	?	?	?	?	?	?
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	?	?
Protoceratops andrewsi	-	-	-	-	-	-	-	-	-	-
Zuniceratops christopheri	-	-	-	-	-	-	-	-	-	-
Diabloceratops eatoni	0	0	0	0	0	0	0	0	0	1
Albertaceratops nesmoi	0	0	0	?	?	?	?	0	0	1
Nasutuceratops titusi	0	?	?	0	?	?	?	1	?	1
Avaceratops lammersi	0	0	?	0	?	?	?	?	?	1
Centrosaurus apertus	0	0	0	0	0	0	0	0	0	1
Centrosaurus brinkmani	0	0	0	0	?	?	?	0	?	1
Rubeosaurus ovatus	?	?	?	0	?	?	?	0	?	?
Styracosaurus albertensis	0	0	0	0	0	0	0	0	0	1
Einiosaurus procurvicornis	0	0	0	0	0	0	0	0	?	1
Achelousaurus horneri	0	0	0	0	0	0	0	0	?	1
Pachyrhinosaurus canadensis	?	?	0	?	?	?	?	0	?	?
Pachyrhinosaurus lakustai	?	?	0	0	?	?	?	0	-	1
Chasmosaurus belli	0	1	1	1	1	1	0	0	-	0
Chasmosaurus russelli	0	1	1	1	1	1	0	0	-	0
Chasmosaurus kaiseni	0	1	1	1	1	1	0	0	-	0
Pentaceratops sternbergi	1	2	1	1	2	2	1	0	-	0
Triceratops horridus	1	0	1	1	1	1	0	1	2	0

taxon	111	112	113	114	115	116	117	118	119	120
Leptoceratops gracilis	-	-	-	-	-	-	-	-	-	-
Bagaceratops rozhdestvenskyi	-	-	-	-	-	-	-	-	-	-
Magnirostris dodsoni	?	?	?	?	?	?	?	?	?	?
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	?	?
Protoceratops andrewsi	-	-	-	-	-	-	-	-	-	-
Zuniceratops christopheri	-	-	-	-	-	-	-	-	-	-
Diabloceratops eatoni	0	0	0	1	0	1	0	0	0	0
Albertaceratops nesmoi	0	0	0	1	0	1	3	0	3	0
Nasutuceratops titusi	0	1	0	0	0	0	0	0	0	0
Avaceratops lammersi	?	1	0	?	?	?	?	?	?	?
Centrosaurus apertus	0	0	1	1	2	2	0	0	0	0
Centrosaurus brinkmani	0	0	0	?	?	?	?	?	?	0
Rubeosaurus ovatus	0	0	0	0	0	0	1	0	1	0
Styracosaurus albertensis	0	0	0	0	0	0	1	1	1	0
Einiosaurus procurvicornis	0	0	0	0	0	0	1	1	0	0
Achelousaurus horneri	0	0	0	1	0	2	1	1	0	0
Pachyrhinosaurus canadensis	?	?	?	?	?	?	?	?	?	?
Pachyrhinosaurus lakustai	0	0	0	1	0	2	1	1	0	0
Chasmosaurus belli	0	0	0	2	1	3	2	2	3	0
Chasmosaurus russelli	0	0	0	2	1	3	2	2	3	0
Chasmosaurus kaiseni	0	0	0	3	1	0	3	0	3	0
Pentaceratops sternbergi	0	0	1	3	1	3	3	0	3	0
Triceratops horridus	0	1	0	4	0	0	4	0	4	0

taxon	121	122	123	124	125	126	127	128	129	130
Leptoceratops gracilis	-	-	-	-	-	-	?	0	?	0
Bagaceratops rozhdestvenskyi	-	-	-	-	-	-	?	?	?	0
Magnirostris dodsoni	?	?	?	?	?	?	?	?	?	0
Turanoceratops tardabilis	?	?	?	?	?	?	?	?	?	?
Protoceratops andrewsi	-	-	-	-	-	-	0	0	0	0
Zuniceratops christopheri	-	-	-	-	-	-	?	?	?	1
Diabloceratops eatoni	1	0	1	0	1	0	?	?	?	1
Albertaceratops nesmoi	1	0	1	0	1	?	?	?	?	1
Nasutuceratops titusi	1	0	1	0	1	1	?	?	?	?
Avaceratops lammersi	?	?	?	?	?	?	1	?	1	1
Centrosaurus apertus	1	0	1	0	1	1	1	?	1	1
Centrosaurus brinkmani	1	0	?	?	?	1	?	?	1	1
Rubeosaurus ovatus	1	?	?	?	?	?	?	?	?	?
Styracosaurus albertensis	1	1	1	1	1	0	?	?	1	1
Einiosaurus procurvicornis	1	0	1	0	1	?	?	?	1	1
Achelousaurus horneri	1	0	1	0	1	0	?	?	1	1
Pachyrhinosaurus canadensis	?	?	?	?	?	?	?	?	1	1
Pachyrhinosaurus lakustai	1	0	1	0	1	2	1	0	1	1
Chasmosaurus belli	0	-	0	-	0	0	?	?	1	1
Chasmosaurus russelli	0	-	0	-	0	0	?	?	1	1
Chasmosaurus kaiseni	0	-	0	-	0	0	?	?	?	?
Pentaceratops sternbergi	0	-	0	-	0	0	?	1	1	1
Triceratops horridus	0	-	0	-	0	1	1	1	1	1

taxon	131	132	133	134	135	136	137	138	139	140
Leptoceratops gracilis	0	0	0	0	-	0	0	0	0	0
Bagaceratops rozhdestvenskyi	?	0	?	?	?	?	?	?	?	?
Magnirostris dodsoni	?	0	?	?	?	?	?	?	?	?
Turanoceratops tardabilis	?	0	?	?	?	?	?	?	?	?
Protoceratops andrewsi	0	0	?	?	?	0	0	0	0	0
Zuniceratops christopheri	1	0	1	0	-	1	0	1	1	?
Diabloceratops eatoni	?	?	?	?	?	?	?	?	?	?
Albertaceratops nesmoi	1	1	0	0	-	1	1	?	1	?
Nasutuceratops titusi	?	?	?	?	?	?	?	1	?	?
Avaceratops lammersi	?	?	0	0	-	1	1	1	1	1
Centrosaurus apertus	1	1	0	1	0	1	1	1	1	1
Centrosaurus brinkmani	?	1	0	1	0	1	1	1	1	1
Rubeosaurus ovatus	?	?	?	?	?	?	?	?	?	?
Styracosaurus albertensis	?	1	0	1	0	?	?	?	?	?
Einiosaurus procurvicornis	1	1	?	?	?	1	1	1	1	?
Achelousaurus horneri	1	1	?	?	?	1	1	1	1	?
Pachyrhinosaurus canadensis	1	1	0	1	1	?	?	?	?	?
Pachyrhinosaurus lakustai	?	1	0	1	1	1	1	1	1	1
Chasmosaurus belli	1	0	1	0	-	1	1	1	1	1
Chasmosaurus russelli	1	0	1	0	-	1	1	1	1	1
Chasmosaurus kaiseni	?	?	?	?	?	?	?	?	?	?
Pentaceratops sternbergi	1	0	1	0	-	1	1	1	1	1
Triceratops horridus	1	0	1	0	-	1	1	1	1	1

taxon	141	142	143	144	145	146	147	148	149	150
Leptoceratops gracilis	0	0	0	0	0	2	?	0	0	0
Bagaceratops rozhdestvenskyi	?	0	?	?	0	0	?	?	?	?
Magnirostris dodsoni	?	0	?	?	?	?	?	?	?	?
Turanoceratops tardabilis	?	1	0	1	1	1	?	?	?	?
Protoceratops andrewsi	?	0	0	0	0	0	0	0	0	0
Zuniceratops christopheri	1	0	0	1	?	1	?	?	?	1
Diabloceratops eatoni	?	?	?	?	?	?	?	?	?	?
Albertaceratops nesmoi	?	?	1	1	1	?	?	?	?	?
Nasutuceratops titusi	?	?	?	?	1	?	?	?	?	?
Avaceratops lammersi	?	?	?	?	1	1	1	1	?	1
Centrosaurus apertus	0	1	1	1	1	1	1	1	1	1
Centrosaurus brinkmani	0	1	1	1	1	1	1	1	1	1
Rubeosaurus ovatus	?	?	?	1	1	1	?	?	?	?
Styracosaurus albertensis	0	?	?	1	1	?	1	1	1	1
Einiosaurus procurvicornis	?	1	1	1	1	1	1	1	1	1
Achelousaurus horneri	?	1	1	1	1	1	?	?	?	1
Pachyrhinosaurus canadensis	?	?	?	1	1	1	?	?	?	?
Pachyrhinosaurus lakustai	0	1	1	1	1	1	1	1	?	1
Chasmosaurus belli	?	1	1	1	1	1	1	1	1	1
Chasmosaurus russelli	?	1	1	1	1	1	1	1	1	1
Chasmosaurus kaiseni	?	1	?	?	?	?	?	?	?	?
Pentaceratops sternbergi	?	1	1	1	1	1	1	1	1	1
Triceratops horridus	1	1	1	1	1	1	1	1	1	1

taxon	151	152	153	154	155
Leptoceratops gracilis	0	0	0	0	0
Bagaceratops rozhdestvenskyi	?	?	?	?	?
Magnirostris dodsoni	?	?	?	?	?
Turanoceratops tardabilis	?	?	?	?	?
Protoceratops andrewsi	0	0	0	0	0
Zuniceratops christopheri	1	0	0	0	1
Diabloceratops eatoni	?	?	?	?	?
Albertaceratops nesmoi	?	?	?	?	?
Nasutuceratops titusi	?	?	?	?	?
Avaceratops lammersi	?	1	0	?	?
Centrosaurus apertus	1	1	0	0	1
Centrosaurus brinkmani	?	1	0	0	?
Rubeosaurus ovatus	?	?	?	?	?
Styracosaurus albertensis	?	1	0	0	1
Einiosaurus procurvicornis	?	1	0	1	1
Achelousaurus horneri	1	?	?	?	?
Pachyrhinosaurus canadensis	?	1	0	?	?
Pachyrhinosaurus lakustai	?	1	0	0	1
Chasmosaurus belli	2	1	0	1	1
Chasmosaurus russelli	2	1	0	1	1
Chasmosaurus kaiseni	?	?	?	?	?
Pentaceratops sternbergi	2	1	0	1	1
Triceratops horridus	2	1	1	1	1

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